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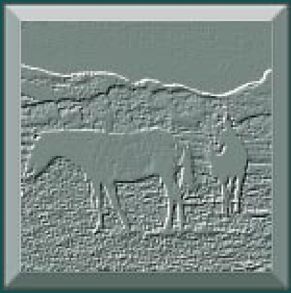

Non-native Species

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Overview

Introduced species evolved elsewhere and have been transported and purposefully or accidentally disseminated by humans. Many synonyms are used to describe these species: alien, exotic, non-native, and nonindigenous. The spread of non-native species during the last century has been unprecedented in Earth's history, with the speed and scale of these infestations more rapid than natural invasions. The spread of non-native species in human-disturbed habitats reflects a deterioration of the North American landscape.

Introduced species disrupt the functioning of native ecosystems upon which humans depend. Many non-native species become pests by rapidly dispersing into communities in which they have not evolved, and by displacing native species because of evolutionary mismatches. For example, non-native species contributed to 68% of the fish extinctions in the past 100 years, and the decline of 70% of the fish species listed in the Endangered Species Act (Lassuy 1994).

As several articles indicate, the economic cost incurred because of non-native species reaches millions, or even billions, of dollars. Non-native species damage agricultural crops and rangelands, contribute to the decline of commercially important fishes, spread diseases that affect domestic animals and humans, and disrupt vital ecosystem functions.

Some species that have become pests were first introduced to "create" a desired landscape; these non-natives include exotic game animals, fish, and decorative plants. Mack and Thompson (1982), for example, traced the widespread dissemination of 139 weedy, non-native plants in the United States to seed catalogues and the commercial seed trade of the 19th century. Similarly, feral (wild) domestic animals such as mustangs are a major problem on public lands, and sound management of such animals has been impeded by romantic images of America's past.

Accidental introductions through human travel is a theme repeated in several articles, indicating that cargo traffic (ship, air, land) is a major vector of non-native species and should be monitored as world trade increases. The zebra mussel (*Dreissena polymorpha*) is the most notorious hitchhiker, but introductions through ballast water are not isolated to the Laurentian Great Lakes. My colleagues and I recently found that 11 exotic benthic invertebrates have become established in Oregon estuaries. Similarly, dinoflagellates causing red tide toxins have spread into Australian waters through cargo traffic. The importation of raw

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logs from New Zealand and Siberia endanger Pacific Northwest forests through forest pests hitchhiking in the bark and wood (J. Lattin, Oregon State University, personal communication). It is clear that international cargo traffic must be monitored to reduce the spread of non-native species.

Although this section only briefly mentions disease, it may be one of the most important problems caused by non-native species. After Columbus landed in the New World, for example, 95% of the Native tribes became extinct because their people were susceptible to European microbes (Diamond 1992). Likewise, exotic diseases have devastated populations of aquatic organisms worldwide, killed many native trees, and exterminated much of Hawaii's avifauna. Non-native species are the primary vector for these diseases; for instance, the spread of fish diseases worldwide resulted from the unprecedented transfer of non-native fishes for hatchery production.

It is clear from the small sampling of articles here that changes caused by non-native species are widespread and profound. We present different case histories representative of a myriad of management problems today. New problems continually arise, however, because humans deliberately and accidentally release non-native species and encourage their invasion through massive disturbances of the landscape, thereby mitigating against native species' resistance to invaders by stressing native populations. These articles should make it clear that although non-native species are costly to manage, manage them we must.

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Non-native Aquatic Species in the United States and Coastal Waters

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Since the European colonization of North America, many non-native aquatic species have been introduced into the United States and adjacent waters. The harm caused by recent introductions, particularly by the zebra mussel (*Dreissena polymorpha*), and concern about a possible increase in the number of unintentional introductions resulted in passage of the Nonindigenous Aquatic Nuisance Prevention and Control Act of 1990. This statute mandates development and implementation of a comprehensive national program to prevent and respond to problems caused by the unintentional introduction of nonindigenous aquatic species into waters of the United States. This article presents an overview of nonindigenous aquatic species, a summary of potential pathways of introduction, and response strategies.

Presence and Distribution

Non-native aquatic species in the United States and coastal waters include species from many plant and animal taxa and span the entire country (Figure). That this problem is extensive is clear by the numbers: 139 nonindigenous species are now established in the Great Lakes (Mills et al. 1993); 32 species of nonindigenous marine organisms were collected from one small Oregon estuary (Carlton 1991); 96 nonindigenous sponges, worms, crustaceans, and other invertebrates are now found in San Francisco Bay (Carlton 1979); and more than half of Hawaii's free-living species are nonindigenous (U.S. Congress 1993). The rate of nonindigenous species' introductions into the Great Lakes has increased in spurts since 1810, largely in response to an expanding human population, development in the basin, and increased transoceanic shipping.

Benefits and Costs

Nonindigenous aquatic species have been both beneficial and problematic. Beneficial aspects include enhancing recreational opportunities such as sport-fishing; providing reliable, high-quality food via aquaculture and mariculture; and aesthetically improving the human environment via the aquarium industry. Recreational fishing contributed an estimated \$24 billion in expenditures and \$69.4 billion in economic output in 1991 (SFI 1994).

Problems associated with nonindigenous aquatic species are primarily related to ecological issues, such as their effects on indigenous species, and financial issues, such as economic losses caused by biofouling of water-intake pipes. For example, nonindigenous species were cited as a contributing cause in the extinction of 27 species and 13 subspecies of North American fishes over the past 100 years (Miller et al. 1989). Federal, state, and local governments, as well as industry, have often borne significant costs related to nonindigenous aquatic species. From 1906 to 1991, estimated losses associated with 79 aquatic and terrestrial nonindigenous species were roughly \$97 billion (Table 1), and worst-case estimates for 15 potential high-impact nonindigenous species project future economic losses of another \$134 billion (U.S. Congress 1993).

Table 1. Estimated cumulative losses to the United States from selected categories of harmful nonindigenous species, 1906-91 (U.S. Congress 1993).

Category	Species analyzed (no.)	Cumulative loss est. ($ millions, 1991)	Species not analyzed (no.)
Plants	15	603	-
Terrestrial vertebrates	6	225	> 39
Insects	43	92,658	> 330
Fish	3	467	> 30
Aquatic invertebrates	3	1,207	> 35
Plant pathogens	5	867	> 44
Other	4	917	-
Total	79	96,944	> 478

Introduction and Dispersal

Many non-native aquatic species have entered the country in infested stock for aquaculture or fishery enhancement. For example, the introduction of the Pacific oyster (*Crassostrea gigas*) to the west coast in the 1920's brought with it a Japanese snail (*Ocenebra japonica*) that preys on native oysters, a flatworm (*Pseudostylochus ostreophagus*), and possibly also a copepod parasite (*Mytilicola orientalis*). An Asian tapeworm (*Bothriocephalus opsarichthydis*) was found in several species of native fish in the 1970's following its introduction via infected grass carp (*Ctenopharyngodon idella*). A non-native freshwater snail (*Potamopyrgus antipodarum*) that probably escaped from a fish aquaculture facility now threatens indigenous mollusks of the Snake River region.

The aquarium industry is a significant entry and dispersal pathway for non-native aquatic species. Hydrilla (*Hydrilla verticillata*), an aquatic weed that causes a major navigation hazard, is believed to have been released by aquarium dealers in an attempt to create a domestic source of the plant (Williams 1980). At least three snail species entered U.S. waters when individual snails were discarded by aquarium dealers or their customers over the past few decades. Since 1980, releases from aquaria were the source of at least seven nonindigenous fish species that are now established, and the aquarium fish industry is believed the source of at least 27 nonindigenous fish species now established in the continental United States (Courtenay and Williams 1992; U.S. Congress 1993).

Another major introduction and dispersal pathway for non-native aquatic species is via ballast water discharge. Since many ports are infested with non-native aquatic species, ballasting operations often bring these species, as well as indigenous species, into the ballast tanks of a vessel. These organisms are then transported around the world within the ballast tanks. When a vessel unloads or picks up cargo, the operator often empties the ballast tanks, thus introducing these organisms into new environments. This mode of introduction is probably responsible for the introduction of zebra mussels, ruffe (*Gymnocephalus cernuus*), and the spiny water flea (*Bythotrephes cederstroemi*) into the Great Lakes (U.S. Congress 1993).

Many non-native aquatic species are intentionally imported as pets, for aquaculture, or to supplement recreational fishing. State and federal natural resource agencies have intentionally introduced a variety of non-native aquatic species to enhance recreational and commercial interests (e.g., brown trout [*Salmo trutta*], carp, and Pacific oyster). Some animals (e.g., water fleas, freshwater shrimp, crayfish, and others; Wildlife Nurseries, Inc. 1989) can be purchased through the mail and introduced outside their natural range. Many tropical aquarium species now found in Florida's waters escaped from aquaculture facilities (Courtenay and Williams 1992). The Aquatic Nuisance Species (ANS) Task Force suggests that it is inevitable that cultured species will eventually escape confinement and enter U.S. waterways.

Assessment and Monitoring

Efforts to assess or monitor non-native aquatic species are, at best, fragmented. Generally, these species are not monitored until they reach nuisance status, such as purple loosestrife (*Lythrum salicaria*) or zebra mussels have, and no broad, nationally coordinated program exists for detecting new species. A nationally coordinated effort for providing timely notification to appropriate entities of the detection and dispersal of all non-native aquatic species is needed. There is currently no definitive evidence to suggest that rates of introduction for non-native aquatic species are increasing or decreasing (Table 2).

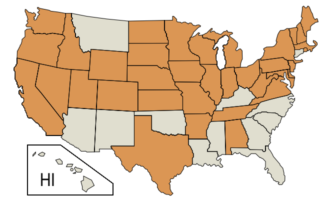
Table 2. Number of new species of foreign origin established per decade (U.S. Congress 1993).

Category	1940-50	1950-60	1960-70	1970-80	1980-90
Terrestrial vertebrates	3	11	13	3	No data
Fish	2	15	18	5	12
Mollusks	5	5	6	10	4
Plant pathogens	3	5	4	16	7

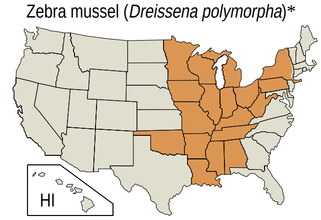
Research Strategies

Three main research strategies are used to limit the damages caused by nonindigenous aquatic species: prevention, control, and detection and monitoring. Prevention relies on the identification and elimination of pathways through which nonindigenous ANS enter the nation's waters. Although prevention should be the first line of defense, it is unlikely to be

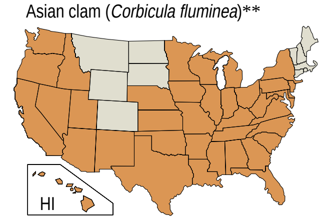
Purple loosestrife (*Lythrum salicaria*)*



Zebra mussel (*Dreissena polymorpha*)*



Asian clam (*Corbicula fluminea*)**



Common carp (*Cyprinus carpio*)**

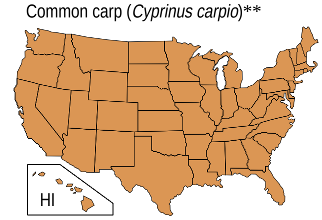


Figure. Distribution of purple loosestrife, Asian clam, zebra mussel, and carp in the United States (shading indicates species presence).
*U.S. Congress 1993.
**U.S. Department of the Interior, National Biological Service 1994. Non-native aquatic species data base.

100% effective and can never eliminate all threats from nonindigenous aquatic species. Therefore, rapid response and control techniques must be identified and in place to control and limit damages caused by nonindigenous ANS. This approach is being used to control ruffe.

Control is intended to reduce the effects of nonindigenous aquatic species through eradication, reduction in numbers to tolerable levels, and exclusion from sensitive areas. Three general control methods exist to prevent the spread of these species: chemical, biological, and physical. Proper evaluation and use of selective chemicals may provide effective control of non-native aquatic species with an apparent minimum of ecological hazard or other side effects. Increasing concern exists, however, about the long-term environmental safety and impacts of chemicals used to control nonindigenous aquatic species. Efforts to control sea lamprey (*Petromyzon marinus*) in the Great Lakes are a prime example of chemical control. This control has been highly successful in reducing the population size of an invading species, but carries an enormous price tag: more than $10 million annually (U.S. Congress 1993).

Carefully planned biological-control programs may provide rapid, cost-effective control and pose negligible ecological problems. The success rate for biological-control programs typically ranges from 16% to 36% (Meyers et al. 1989) and improperly screened biological-control agents have themselves become nuisance species in the past (e.g., blue tilapia [*Tilapia aurea*]; McClelland 1992).

Although often very expensive, physical control of aquatic nuisance species can be an appropriate technique in certain circumstances. Physical control has been used to control nuisance aquatic weeds like Eurasian watermilfoil (*Myriophyllum spicatum*).

Since no single method is likely to provide the necessary level of control, a comprehensive, integrated control strategy combining techniques is usually necessary for an effective control program. Few, if any, control methods are without some environmental risk. When properly used, and with continual monitoring for effectiveness and ecological side effects, environmentally sound control of at least some aquatic nuisance species can be achieved, as in the Great Lakes sea lamprey control program.

Detection and monitoring strategies serve as early warning systems that first identify new invasions and then track ranges and populations. This strategy complements or integrates prevention and control to allow for early intervention and assessment of management actions. The capability for early detection of new invasions will allow managers to implement strategies for limiting their spread and reducing negative effects. Timely detection of non-native aquatic species that are or could become nuisances can also help identify gaps in prevention procedures. Monitoring of those organisms will not only allow rapid response if harmful situations arise but will also allow verification or repudiation of assumptions that may have been made during assessments before intentional releases.

Because of extremely limited resources, cooperative ventures and collaborations between agencies are essential for collecting monitoring information. The Detection and Monitoring Committee of the ANS program is developing a national network to coordinate and provide information regarding occurrences of known nonindigenous aquatic species. This network is intended to provide managers and researchers with an important tool for determining the status of a particular nonindigenous aquatic species, its potential and known effects, and proven or potential control techniques.

By and large, three interrelated problems associated with nonindigenous ANS remain unsolved: (1) determining levels of acceptable risk; (2) setting thresholds or other variables above which more formal decision making and costly approaches for control are invoked; and (3) identifying trade-offs in terms of costs and economic ramifications in the face of uncertainty as to probable success in controlling ANS. Current federal methods and programs to identify risks of potentially harmful nonindigenous aquatic species have many shortfalls—including long response times.

Summary

Nonindigenous aquatic species are widespread in the United States. While many of these organisms have been intentionally introduced, many others dispersed via unintended introductions. The potential for ecological and economic harm resulting from introductions of nonindigenous aquatic species can be large. For example, zebra mussels seem to be jeopardizing a number of native North American mussel species (Williams et al. 1993) and could result in economic losses in excess of $3 billion (U.S. Congress 1993). The actual extent of problems associated with non-native aquatic species remains largely unknown. The ability to detect new species and limit their dispersal before they become problematic is critical if we are to limit future nonindigenous species problems.

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Nonindigenous Fish

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Within the United States alone, humans have intentionally or unintentionally introduced more than 4,500 species of terrestrial and aquatic species to areas outside their historical range (U.S. Congress 1993). Although many terrestrial introductions are viewed as beneficial to humans because of economic and social considerations, all but a few intentional aquatic introductions have proven to be mixed blessings (Courtenay and Williams 1992; Steirer 1992; U.S. Congress 1993). No unintentional aquatic introductions have been considered beneficial (Steirer 1992); instead, their environmental consequences are generally harmful and sometimes catastrophic (Taylor et al. 1984; U.S. Congress 1993).

Both intentional and unintentional introductions have enabled nonindigenous fish to become temporary, and often permanent, residents in nearly every U.S. aquatic system. Complete eradication or exclusion is neither economically plausible nor socially justified (U.S. Congress 1993); therefore, nonindigenous fish are and will continue to be components of these aquatic systems. Because nonindigenous fish have the potential to alter significantly the U.S. aquatic ecosystems during the next century and beyond, their interactions within the aquatic community must be monitored and analyzed to ensure that effective management actions are taken before a crisis arises.

To help document the consequences of nonindigenous fish introductions, the National Biological Service monitors the status and distribution of these organisms in U.S. waters (Williams and Jennings 1991). Since 1978, reports and specimens of various nonindigenous fish have been collected, verified, and entered in a geographic information system, which is a computerized mapping and data base system.

Obtaining qualitative and quantitative information on nonindigenous fish for a national assessment requires cooperation by many agencies, organizations, and individuals (Boydstun and Benson 1992). We collect much of our ecological and geographical data using a voluntary reporting form. Historical accounts are gathered through review of both scientific and other literature, including natural resource agency publications that often provide accounts of nonindigenous fish, stockings, and discoveries. For our purposes, we established a historic cut-off date for usable nonindigenous fish reports at 1800.

We limited this analysis to only reports of nonindigenous fish from open waters identifiable to species level and recognizable nonindigenous hybrids.

Status of Nonindigenous Fish

We have collected more than 11,000 reports that document 404 unique fish species or hybrids introduced outside their native ranges within U.S. waters. This diverse group of 67 families of fish includes species from every continent except Antarctica. Of the 404 species, 252 (62%) are native to the United States but found outside their native ranges, and 152 (38%) are from other countries. Nonindigenous hybrid fish represent roughly 5% (19) of the total 404 nonindigenous fish species.

Our total is considerably higher than the 127 nonindigenous fish (70 U.S. and 57 non-U.S.) reported in the United States in 1992 by the Office of Technology Assessment (U.S. Congress 1993). Courtenay and Williams (1992) reported 99 exotic (non-U.S.) nonindigenous fish species in the contiguous U.S. waters in 1992, of which 46 were established as sustaining populations. The disparity between our results and these estimates is most influenced by our intent to include all reported nonindigenous fish that have been found within the United States since 1800, regardless of their current status.

Game and associated forage fish are the most widely distributed nonindigenous fish. These include the salmonids (salmon and trout), ictalurids (catfish), centrarchids (bass and sunfish), percids (walleye and sauger), and cyprinids (minnows). The two most widely distributed nonindigenous fish species are goldfish (*Carassius auratus*) and common carp (*Cyprinus carpio*). Both have been reported or collected from all states except Alaska (Table). Goldfish introductions are the result of the release of bait and aquarium fish and forage fish stocking for game fish. Widespread distribution of common carp is primarily due to the stocking program of the U.S. Fish Commission in the late 1800's and early 1900's and later use of juvenile carp as bait.

Reported Occurrences

All 50 states have reported nonindigenous fish from their open waters (Fig. 1). When considering total diversity of nonindigenous fish species, the top five states are California (114), Texas (96), Florida (96), North Carolina (83), and Nevada (82). In fact, of the total 404 species, 312 (77%) are reported as occurring or having been found within the 11 states crossing or below the 35th parallel (e.g., Hawaii, California, Arizona, New Mexico, Texas, Oklahoma, Arkansas, Louisiana, Alabama, Georgia, and Florida). Although Hawaii was historically without any native freshwater fish, it now has 52 nonindigenous freshwater fish species.

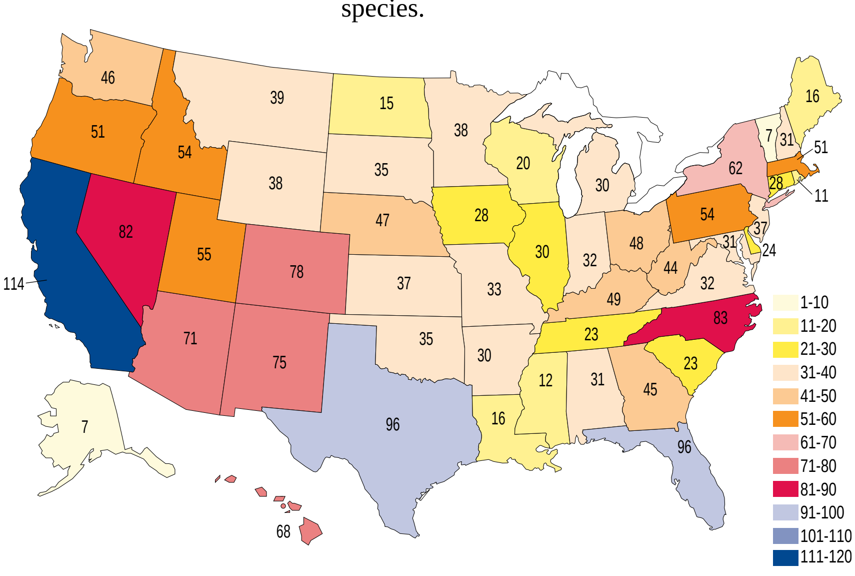

Fig 1. The number of nonindigenous fish species reported by state, 1800-1994. Some species may not be established or have been eradicated.

Table. Nonindigenous fish introduced into 10 or more states, 1800-1994.

Common name (scientific name)	No. of states reported outside native range
Goldfish (*Carassius auratus*)	49
Common carp (*Cyprinus carpio*)	49
Brown trout (*Salmo trutta*)	47
Rainbow trout (*Oncorhynchus mykiss*)	47
Grass carp (*Ctenopharyngodon idella*)	44
Largemouth bass (*Micropterus salmoides*)	41
Walleye (*Stizostedion vitreum*)	40
Smallmouth bass (*Micropterus dolomieu*)	38
Brook trout (*Salvelinus fontinalis*)	36
White crappie (*Pomoxis annularis*)	36
Bluegill (*Lepomis macrochirus*)	33
Northern pike (*Esox lucius*)	33
Striped bass (*Morone saxatilis*)	32
Green sunfish (*Lepomis cyanellus*)	31
Black crappie (*Pomoxis nigromaculatus*)	31
Yellow perch (*Perca flavescens*)	29
Channel catfish (*Ictalurus punctatus*)	29
Coho salmon (*Oncorhynchus kisutch*)	28
Rock bass (*Ambloplites rupestris*)	26
Lake trout (*Salvelinus namaycush*)	26
Threadfin shad (*Dorosoma petenense*)	26
Western mosquitofish (*Gambusia affinis*)	25
Fathead minnow (*Pimephales promelas*)	24
Rainbow smelt (*Osmerus mordax*)	23
Chinook salmon (*Oncorhynchus tshawytscha*)	22
White bass (*Morone chrysops*)	22
Atlantic salmon (*Salmo salar*)	22
Golden shiner (*Notemigonus crysoleucas*)	21
Redear sunfish (*Lepomis microlophus*)	20
Muskellunge (*Esox masquinongy*)	20
Sockeye salmon (*Oncorhynchus nerka*)	19
Pumpkinseed (*Lepomis gibbosus*)	19
Blue catfish (*Ictalurus furcatus*)	19
Alewife (*Alosa pseudoharengus*)	18
Tench (*Tinca tinca*)	18
Rudd (*Scardinius erythrophthalmus*)	18
American shad (*Alosa sapidissima*)	17
Brown bullhead (*Ameiurus nebulosus*)	15
Chain pickerel (*Esox niger*)	15
Flathead catfish (*Pylodictis olivaris*)	15
Black bullhead (*Ameiurus melas*)	15
Spotted bass (*Micropterus punctulatus*)	15
Warmouth (*Lepomis gulosus*)	15
Lake whitefish (*Coregonus clupeaformis*)	14
Cutthroat trout (*Oncorhynchus clarki*)	14
White catfish (*Ameiurus catus*)	14
Bighead carp (*Aristichthys nobilis*)	13
Arctic grayling (*Thymallus arcticus*)	13
Mozambique tilapia (*Tilapia mossambica*)	13
Redbreast sunfish (*Lepomis auritus*)	13
Guppy (*Poecilia reticulata*)	12
Piranha (*Serrasalmus* spp.)	12
Blue tilapia (*Tilapia aurea*)	12
Tiger muskellunge (*Esox lucius* x *masquinongy*)	12
Golden trout (*Oncorhynchus aguabonita*)	11
White perch (*Morone americana*)	10
Green swordtail (*Xiphophorus helleri*)	10
Sauger (*Stizostedion canadense*)	10
Redbelly tilapia (*Tilapia zilli*)	10

Trends

The first fish translocation effort began in the early 1870's with an attempt to introduce several eastern species to the west coast and to stock chinook salmon in the East. Fish that were introduced to the West included eels, brook and lake trout, lake whitefish, northern pike, striped bass, American shad, yellow perch, catfish, bullheads, sunfish, black bass, and crappies. Most of these introductions resulted in established populations that still persist today. At this same time brown trout, tench, and carp were being stocked throughout the country. A resurgence of stocking occurred around 1950 when many state agencies began stocking game fish. The popularity of home aquaria and the availability of foreign fish have also contributed to an increase in the number of species introduced in the past 40 years (Courtenay and Williams 1992; Fig. 2).

The Future

The presence of nonindigenous fish will continue to alter U.S. aquatic resources. These species compete with or prey on native game and nongame fish, often with severe negative effects on aquatic ecosystems. Nonindigenous fish that survive the initial introduction and subsequently become established are often tolerant of adverse or altered environmental conditions, including habitat disturbance. This tolerance has been used to justify nonindigenous fish introductions rather than to restore disrupted environments. The environmental tolerance of nonindigenous fish combined with increasing habitat disruption in streams and lakes assures their continued dispersal into formerly unoccupied areas. If the introduction and establishment of nonindigenous fish continue at their present rates, distribution and survival of native aquatic organisms could be drastically affected. These introductions can also profoundly change biological diversity and composition of habitats and ecosystems, which could result in substantially increased rates of extinction of native aquatic species.

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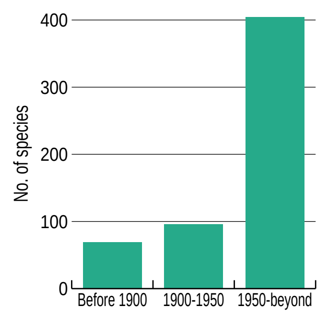

Fig. 2. Diversity of fish introductions over time.

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Non-native Reptiles and Amphibians

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Interest in established, non-native species of reptiles and amphibians in the United States (including territories and possessions) has been increasing the past quarter-century. Concerns regarding the interactions of introduced and native species have driven this interest (Wilson and Porras 1983). Most successful introductions have taken place in the southern tier of states (California to Florida) and on islands. This success rate is probably due, in part, to favorable environmental conditions. Movements by indigenous peoples to islands also may have substantially augmented existing faunas. For example, in American Samoa, virtually the entire terrestrial reptile fauna may have been introduced by the original human colonizers (T.D. Schwaner, Alabama School of Science and Math, personal communication). Since many species of reptiles and amphibians on islands could be considered as introduced, the scope of this report, for islands, is restricted to those introductions that occurred after contact with western societies and for the mainland United States, within the past century. A review of both successful and unsuccessful reptile and amphibian introductions in North America is presented by Smith and Kohler (1977).

Of the documented 53 established non-native amphibian and reptile species (Table), at least 5—spectacled caiman (*Caiman crocodilus*), marine toad (*Bufo marinus*), African clawed frog (*Xenopus laevis*), bullfrog (*Rana catesbeiana*), and brown tree snake (*Boiga irregularis*)—have been established at least 30 years and have been sufficiently monitored to enable preliminary assessment of impacts on the native biota. The marine toad is established in Florida, Hawaii, the Territories of Guam, U.S. Virgin Islands, and American Samoa, and the Commonwealths of Puerto Rico and of the Northern Mariana Islands, where it is regarded as a nuisance species. The spectacled caiman is established in Puerto Rico and Florida, where it may be negatively affecting vertebrates. The African clawed frog is established in Arizona and California, but is not demonstrating any apparent negative effects on native vertebrates. The bullfrog is widely established in western North America, Hawaii, and Puerto Rico, and is implicated in restricting the range of native North American ranid frogs and the Mexican garter snake (*Thamnophis eques*). The brown tree snake is established on Guam and is identified as the agent in the extirpation of native forest-dwelling birds and small reptiles.

Courtesy G. Rodda, NBS

Marine toad (*Bufo marinus*).

Table. Established exotic species of amphibians and reptiles in the United States (including territories and possessions).

Scientific name (common name)	Area (reference) [a]
Frogs and toads	
Bufo marinus (marine toad)[b]	FL (Ashton and Ashton 1988; Wilson and Porras 1983), MP (Rodda et al.1991), GU McCoid 1993), HI (McKeown 1978), AS (Amerson et al. 1982), PR[c], VI[c]
Dendrobates auratus (poison-dart frog)	HI (McKeown 1978)
Eleutherodactylus coqui (common coqui)	FL, LA, VI (Conant and Collins 1991)
E. planirostris (greenhouse frog)	FL, LA (Conant and Collins 1991)
Litoria fallax (eastern dwarf treefrog)	GU, MP? (McCoid 1993)
Osteopilus septentrionalis (Cuban treefrog)	FL (Ashton and Ashton 1988; Conant and Collins 1991)
Rana catesbeiana (bullfrog)[d]	HI, PR, western U.S. except ND and MN (Conant and Collins 1991; McKeown 1978)
R. pipiens (northern leopard frog)[d]	CA (Stebbins 1985)
R. rugosa (wrinkled frog)	HI (McKeown 1978)
Xenopus laevis (African clawed frog)	CA, AZ, NC?[e],VA?[f] (McCoid and Fritts 1980b)
Salamanders	
Ambystoma tigrinum (tiger salamander)[d]	CA, AZ (Stebbins 1985)
Lizards	
Ameiva ameiva (South American ground lizard or giant ameiva)	FL (Ashton and Ashton 1988; Conant and Collins 1991)
Anolis carolinensis (green anole)[d]	CA (Bury and Luckenbach 1976), GU (McCoid 1993), HI (McKeown 1978), MP (Rodda et al. 1991)
A. chlorocyanus (Hispaniolan green anole)	FL[g]
A. cristellatus (Puerto Rican crested anole)	FL (Ashton and Ashton 1988; Conant and Collins 1991)
A. cybotes (large-headed anole)	FL (Ashton and Ashton 1988; Conant and Collins 1991)
A. distichus (bark anole)	FL (Ashton and Ashton 1988; Conant and Collins 1991)
A. equestris (knight anole)	FL (Ashton and Ashton 1988; Conant and Collins 1991)
A. garmani (Jamaican giant anole)	FL (Ashton and Ashton 1988; Conant and Collins 1991)
A. sagrei (brown anole)	FL, TX (Ashton and Ashton 1988; Conant and Collins 1991), LA (Thomas et al. 1990)
Basiliscus vittatus (brown basilisk)	FL (Ashton and Ashton 1988; Conant and Collins 1991)
Carlia fusca (brown four-fingered skink)	GU (McCoid 1993), MP (Rodda et al. 1991)
Chamaeleo jacksonii (Jackson's chameleon)	HI (McKeown 1978)
Cnemidophorus lemniscatus (South American whiptail)	FL (Ashton and Ashton 1988; Conant and Collins 1991)
Cyrtopodion scabrum (roughtail gecko)	TX (Conant and Collins 1991)
Ctenosaura pectinata (Mexican spiny-tailed iguana)	FL, TX (Conant and Collins 1991)
Gekko gekko (tokay gecko)	FL (Ashton and Ashton 1988; Conant and Collins 1991)
Gonatodes albogularis (yellow-headed gecko)	FL (Ashton and Ashton 1988; Conant and Collins 1991)
Hemidactylus frenatus (house gecko)	GU (McCoid 1993), MP (Rodda et al. 1991), HI (McKeown 1978), AS (Amerson et al. 1982), FL (Meshaka et al. 1994).
H. garnotii (fox gecko)	FL (Ashton and Ashton 1988; Conant and Collins 1991)
H. mabouia (cosmopolitan house gecko)	FL (Butterfield et al. 1993; Lawson et al. 1991)
H. turcicus (Mediterranean house gecko)	AZ (Stebbins 1985), NM (Painter et al. 1992), AR (Paulissen and Buchanan 1990), NV (Saethre and Medica 1993), FL (Ashton and Ashton 1988), TX, OK, LA, AL, MS, GA, PR (Conant and Collins 1991)
Iguana iguana (green iguana)	FL (Conant and Collins 1991), HI (McKeown 1978), PR[c]
Lamprolepis smaragdina (green tree skink)	MP (Rodda et al. 1991)
Leiocephalus carinatus (carinate curly-tailed lizard)	FL (Ashton and Ashton 1988; Conant and Collins 1991)
L. schreibersii (Schreiber's curly-tailed lizard)	FL (Conant and Collins 1991)
Lampropholis delicata (rainbow skink)	HI (Baker 1979)
Phelsuma sp. (day gecko)	HI[h]
Phrynosoma cornutum (Texas horned lizard)[i]	LA, FL, GA (Ashton and Ashton 1988; Conant and Collins 1991)
Podarcis muralis (common wall lizard)	OH (Conant and Collins 1991)
P. sicula (Italian wall lizard)	NY, KS (Conant and Collins 1991)
Sphaerodactylus argus (ocellated dwarf gecko)	FL (Ashton and Ashton 1988; Conant and Collins 1991)
S. elegans (ashy gecko)	FL (Ashton and Ashton 1988; Conant and Collins 1991)
S. notatus (reef gecko)[j]	FL (Conant and Collins 1991)
Snakes	
Boiga irregularis (brown tree snake)	GU (Fritts 1988), MP?[k]
Rhamphotyphlops braminus (Brahminy blind snake)	FL (Ashton and Ashton 1988; Conant and Collins 1991)
Turtles	
Apalone spinifera (spiny softshell turtle)[d]	CA (Stebbins 1985), AZ[l]
Chelydra serpentina (snapping turtle)[d]	CA, NV?, UT? (Bury and Luckenbach 1976; Stebbins 1985), AZ[l]
Palea steindachneri (wattle-necked softshell turtle)	HI (Ernst and Barbour 1989)
Pelodiscus sinensis (Chinese softshell turtle)	GU (McCoid 1993), HI (McKeown 1978)
Terrapene carolina (common box turtle)[d]	GU? (McCoid 1993)
Trachemys scripta (common slider)[d]	GU, MP? (McCoid 1993), HI (McKeown 1978), CA, AZ (Stebbins 1985)
Alligators and crocodiles	
Caiman crocodilus (spectacled caiman)	FL, PR (Ashton and Ashton 1988; Conant and Collins 1991)

[a] Area abbreviations conform to the United States Postal Service; uncommon usages are Commonwealth of the Northern Mariana Islands — MP, Guam —GU, American Samoa — AS, U.S. Virgin Islands — VI, Puerto Rico — PR.
[b] Native range in United States is extreme southern Texas.
[c] R. Henderson, Milwaukee Public Museum, personal communication.
[d] Native range is eastern North America.
[e] M. McCoid, Texas A & M University-Kingsville, unpublished data.
[f] R. Tinsley, University of Bristol, personal communication.
[g] J. Collins, University of Kansas, personal communication.
[h] L. Nakahara, Hawaii Department of Agriculture, personal communication.
[i] Native range is south-central United States.
[j] Native range is Florida Keys.
[k] T. Fritts, National Biological Service, personal communication.
[l] C. Schwalbe, University of Arizona, personal communication.

Case Studies

Spectacled Caiman

The spectacled caiman has been established in southern Florida for about 30 years (Ellis 1980). There are few published accounts of this species in Florida, but one (Ellis 1980) indicated that these animals eat fish, amphibians, and mammals. This information, coupled with the species' ability to tolerate crowding in bodies of water and relatively rapid maturation, suggests that impacts on native alligators (*Alligator mississippiensis*) might be expected (C.M. Sekerak, University of South Florida, personal communication). Studies in the species' native range (J. Dixon, Texas A&M University, personal communication), however, suggest that the spectacled caiman does not co-occur with larger species of crocodilians, perhaps because of their predation on the smaller caimans. Since the American alligator reaches a larger size than the spectacled caiman, it is possible that the American alligator will deter the caiman from substantially expanding its range.

Marine Toad

The marine toad, native to the tropical New World, is widely introduced and now has a virtually circumtropical range (Zug and Zug 1979). Populations were originally established for insect control, but the species itself became a pest. Information from Australia (Tyler 1989) indicates that ingestion of marine toads, because they have highly toxic skin glands, results in deaths of native reptiles, birds, and mammals. Observations on Guam, where the marine toad has been established since 1937 (McCoid 1993), indicate that poisonings of pet dogs and cats by biting or mouthing marine toads are relatively common (R. Dorner, Marianas Veterinary Clinic, personal communication). On Guam, the island-wide decline of a large varanid lizard is attributed to its predation on the introduced toad (McCoid et al. 1994). In Florida, where the marine toad has been established since 1955, poisonings of pets (Ashton and Ashton 1988) and declines of native amphibians in areas of co-occurrence with the marine toad are reported (J. Rossi, Jacksonville University, personal communication). In a laboratory situation, a native toad (*Bufo americanus*) was behaviorally dominated and excluded from feeding by marine toads (Boice and Boice 1970). There is a literature survey on the marine toad that includes information on extralimital populations (Lawson 1987).

African Clawed Frog

Despite initial fears of the effect of the African clawed frog on aquatic California vertebrates (St. Amant 1975), a subsequent study (McCoid and Fritts 1980a) indicated that these fears may be unwarranted because the only vertebrates found in stomach analyses were immature African clawed frogs and an introduced fish species. Other studies (McCoid and Fritts 1980b, 1993) characterize populations as living primarily in temporary and artificial bodies of water, where most native aquatic vertebrates are expected to be absent. Recently, populations in southern California may have declined because of drought (McCoid et al. 1993). Although African clawed frogs have been established in California since the mid-1960's (McCoid and Fritts 1980b), impacts on native invertebrates, their primary food source, are unassessed.

Bullfrog

Although precise dates of introductions of the bullfrog into many areas of western North America are not well known (Bury and Whelan 1984), the earliest introduction occurred in 1896 (Hayes and Jennings 1986). Impacts on native ranid frogs, however, are well documented and may account for range restrictions of native ranids (Moyle 1973; Hayes and Jennings 1986; Stuart and Painter 1993). Recent information indicates that the Mexican garter snake is also declining because of predation by bullfrogs (*see* Rosen and Schwalbe, this section).

Brown Tree Snake

Since the introduction of the brown tree snake on Guam about 40 years ago, the snake has reached enormous densities (Rodda et al. 1992) and is implicated in the demise of the entire native forest-dwelling bird community (Savidge l987) and some of the larger lizard species (Rodda and Fritts 1992). Additional impacts include disruption of electrical power (Fritts et al. 1987), predation on domesticated animals (Fritts and McCoid 1991), and human health risks (Fritts et al. 1990, 1994). There are several overviews of the brown tree snake problem on Guam (Fritts 1988; McCoid 1991; also *see* Fritts and Rodda, this section).

Discussion and Summary

Exotic species of reptiles and amphibians are established in the following areas of the United States (Table): Florida (30 species), Hawaii (12), Guam (9), Commonwealth of the Northern Mariana Islands (8), California (6), Louisiana (5), Puerto Rico (5), Texas (4), and Arizona (3). All other areas combined have 9 species. Many of these introductions are due to released or escaped pets.

The ability to assess impacts of exotics on native species may be related, in part, to the length of time that the exotic has been established. For example, deleterious impacts by the brown tree snake on Guam were not noticed by biologists until about 25 years after initial colonization (Savidge 1987). Thus, short-term studies of many non-native reptiles and amphibians may not reveal impacts on native biota. Of the five long-term infestations discussed earlier, only the African clawed frog seems to have not affected the native vertebrate biota. The four detrimental case studies suggest, however, the trend that introduced reptiles and amphibians, like many other introductions, negatively affects established biota. Importantly though, populations of most introduced species of reptiles and amphibians remain unstudied and long-term effects are largely unassessed.

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Non-native Birds

by
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Two of the three most common nesting species in North America today are birds whose ancestors were brought here from Europe. Some non-native birds are more conspicuous than others, so comparisons are only relative, but according to the two largest continental surveys, non-native species (excluding house finches) constitute, on average, about 6% of the bird population during the summer months (Breeding Bird Survey [BBS]) and about 8% in winter (Christmas Bird Count). Percentages vary considerably by habitat and geographic location.

Many exotic bird species were introduced to the United States by European colonists who missed the familiar birds of their homeland and tried to establish populations of familiar Old World species. Farmers also saw opportunities for pest control by birds such as starlings and house sparrows, but they did not anticipate the degree to which these exotic species would outcompete native birds for nesting sites. Most introductions, however, were by sporting or hunting organizations and state game departments that wished to provide more hunting opportunities.

Competition between exotic and native species has been particularly severe on islands. In the Hawaiian Islands, introduced songbird species far exceed native ones. Visitors to Honolulu, for example, see only exotic songbirds unless they hike mountain trails in search of the few remaining endemic species. MacArthur and Wilson (1967) predicted that for every new species colonized or introduced on an island, an average of one species will become extinct. Even Puerto Rico has breeding populations of about 20 kinds of exotic songbirds, far outnumbering the endemics.

The best-known introductions in North America are those that were highly successful: the house sparrow (*Passer domesticus*), European starling (*Sturnus vulgaris*), rock dove or common pigeon (*Columba livia*), ring-necked pheasant (*Phasianus colchicus*), mute swan (*Cygnus olor*), gray or Hungarian partridge (*Perdix perdix*), and the chukar (*Alectoris chukar*). They readily adapted to their new environments, and most have prospered here for more than 100 years.

Data Sources

Before the mid-20th century, information on the distribution and population trends of exotic birds came primarily from scattered accounts in the literature, from state bird books, and from the Audubon Christmas Bird Count (CBC). Since 1966 in the eastern states and Canada, and 1968 in the West, the BBS (Robbins et al. 1986) has provided information on geographic distribution, relative abundance, and population trends for all but the rarest species. A condensed summary of BBS trends of exotic species (Table) based on as many as 2,500 fifty-stop roadside transects per year is presented for the three major regions of the continent.

History and Status

Cattle Egret (*Bubulcus ibis*)

The only records of intentional release of this African species in the United States are from Hawaii, where the bird was deliberately introduced on five major islands in July and August 1959 to control flies around homes and cattle (Breeze 1959). These birds were obtained in Florida, where they arrived in the early 1940's from South America by way of the West Indies. The species had been known from British Guiana since the 1870's (American Ornithologists' Union 1983), but no firm documentation of its arrival there from Africa is known. The species' spread across the continental United States is well documented by the BBS (Table) and the CBC. The cattle egret is highly migratory, and many of the American birds winter in Latin America. Cattle egrets feed primarily in pastures with cattle. Concerns that cattle diseases might be carried across international boundaries have so far lacked documentation, but populations are being monitored and movements of banded birds are being tracked.

Waterfowl

Many species of exotic waterfowl have found their way into the wild through intentional introductions and by escaping from captivity. The large, heavy-bodied muscovy duck (*Cairina moschata*) from Mexico, in both natural and white plumage, is a common sight in many city parks, but is less commonly found in the wild where it must forage for itself. Many European and some Asiatic ducks, and even a few exotic geese, escape from private collections, especially during storms. Because the number of these individuals is small, their populations have not been monitored.

Table. Population trends from the Breeding Bird Survey, 1966-92. Dashes under "Population trend" indicate insufficient data; dashes under "Significance" indicate no significant changes.

Species	Population trend		Significance*	
	1966-79	1980-92	1966-92	1966-92
Cattle egret				
East	Increase	Stable**	Stable**	-
Center	Increase	Decrease	Increase	-
Continent	Increase	Decrease	Increase	-
Mute swan				
East	-	Increase	Increase	$P < 0.05$
Continent	-	Increase	Increase	$P < 0.05$
Ring-necked pheasant				
East	Decrease	Increase	Decrease	-
Center	Stable**	Decrease	Stable**	-
West	Stable**	Decrease	Decrease	-
Continent	Decrease	Stable**	Decrease	-
Gray partridge				
East	Decrease	-	Decrease	-
Center	Increase	Decrease	Increase	-
West	-	Decrease	Decrease	-
Continent	Increase	Stable**	Increase	-
Rock dove				
East	Increase	Stable**	Increase	-
Center	Increase	Decrease	Stable**	-
West	Increase	Increase	Increase	-
Continent	Increase	Decrease	Increase	-
European starling				
East	Decrease	Stable**	Decrease	$P < 0.01$
Center	Increase	Decrease	Stable**	-
West	Increase	Decrease	Decrease	-
Continent	Stable**	Stable**	Decrease	$P < 0.05$
House sparrow				
East	Decrease	Decrease	Decrease	$P < 0.001$
Center	Stable**	Decrease	Decrease	$P < 0.001$
West	Increase	Decrease	Stable**	-
Continent	Stable**	Decrease	Decrease	$P < 0.001$

*Probability values are given for those species with a significant continuing decline for the entire survey period.
**Less than 1% change per year on average.

The mute swan of Eurasia is the notable exception. Introduced on Long Island and the lower Hudson Valley of New York in the late 1800's (Bump 1941), this swan is now locally common around Long Island Sound, in the Maryland portion of Chesapeake Bay, and in the Great Lakes region. Small populations thrive in other localities. Recent population increases (Table) and the resulting destruction of submerged aquatic vegetation needed by native waterfowl are causing concern.

Upland Game Birds

Most exotic birds imported for release are nonmigratory gallinaceous species: pheasants and francolins from Asia and partridges from Europe. Most were released to provide more hunting opportunities. Some states, such as Oregon, still have active introduction programs.

The only two Old World species to have become established widely enough to be monitored by the BBS are the ring-necked pheasant and the gray (Hungarian) partridge (Table). The first successful release of ring-necked pheasants was the release of 199 pairs in the Willamette Valley of Oregon in 1881 (Bump and Robbins 1966). Ring-necked pheasants have become an important game species in the northern states, but have had detrimental effects on remnant populations of the greater prairie chicken (*Tympanuchus cupido*; Vance and Westemeier 1979). Gray partridges have been in America since 1908-09, when nearly 40,000 birds, mostly wild-trapped in Hungary, were released in the United States and Canada (Bump and Robbins 1966).

Doves

The domestic pigeon or rock dove was first introduced from Europe by French settlers in the early 1600's (Schorger 1952). Now they are one of the most noticeable birds in American cities and farming communities. Countless thousands are still reared annually by pigeon fanciers who use them for homing and racing competitions, and each year the feral population is supplemented by captive-reared individuals that fail to return home. Rock dove populations were ignored by scientists and bird watchers before the Breeding Bird Survey began in 1966 and were not reported on Christmas Bird Counts until 1974. The population appears to have stabilized following a sharp increase in the 1960's and 1970's (Table).

Introductions of several other dove species have been successful locally, especially in the mild climates of Florida, California, and Hawaii, but these species are not sufficiently widespread to be monitored by existing surveys. The spotted or lace-necked dove (*Streptopelia chinensis*) of eastern Asia was well established in the Hawaiian Islands before 1900, and local populations have been established in southern California since 1917 (Willet 1933). The species now also occurs on St. Croix in the Virgin Islands (Raffaele 1989).

Likewise, the small barred or zebra dove (*Geopelia striata*) was brought to the Hawaiian Islands in 1922, and by 1936-37 it was common on all the major islands except Hawaii. Ten years later the Hawaiian population was estimated at 237,000 birds (Schwartz and Schwartz 1949).

The ringed turtle-dove or Barbary dove (*Streptopelia risoria*) has been domesticated so long that its origin is uncertain. Small populations are established in southern California, eastern Texas, Florida, and Puerto Rico. Occasional individuals occur each year in more northern states. A close relative, the Eurasian collared-dove (*S. decaocto*), has bred in southern Florida since the late 1970's (Smith 1987) and has been found as far north as Louisiana and Georgia. Its rapid spread across Europe in the past few decades suggests its potential for rapid expansion in America.

Parrots

Many species of parrots imported for the cagebird trade have escaped, especially at ports of entry. The budgerigar (*Melopsittacus undulatus*) from Australia and the canary-winged parakeet (*Brotogeris versicolurus*) from South America have established populations in southern Florida and Puerto Rico, while the parakeet has become established in Los Angeles County, California. Of greater concern to orchardists has been the survival and reproduction in more northern states of monk parakeets (*Myiopsitta monachus*) from temperate South America (Bull 1975). Control measures have eliminated most populations of this exotic species in the United States.

Songbirds

Berger (1981) includes accounts of 37 exotic songbird species that maintain breeding populations in Hawaii, and Raffaele (1989) lists 19 that are breeding or probably breeding in Puerto Rico. Fewer nest on the U.S. mainland. The two most notorious species that dominate the environment and have negative effects on native species are the house sparrow and European starling, both of which compete with native birds for nesting cavities.

One hundred house sparrows from England established the first breeding population in New York City in 1851-52. Additional introductions helped the population spread westward to the Mississippi River by 1870, and by 1910, this species was established across the continent (Robbins 1973). Their numbers continued to expand until the automobile replaced the horse and the supply of waste grain was markedly reduced. Their decrease since the mid-1960's is well documented by the BBS (Table).

Sixty European starlings released in New York City in April 1890 (Cruickshank 1942) were the ancestors of the millions that now occupy the American countryside. Although these birds consume enormous quantities of noxious insects and weed seeds, they are serious competitors with native species for nesting cavities and food. Fortunately, their populations seem to have peaked and are now declining (Table).

The house finch (*Carpodacus mexicanus*), native to the western states, is an adaptable species that has rapidly colonized the East since the illegal release of the species on Long Island, New York, in the early 1940's. The birds now breed in every eastern state.

Migratory Immigrants

In addition to birds intentionally released in North America, two migratory species, the cattle egret (already discussed) from Africa and the parasitic shiny cowbird (*Molothrus bonariensis*) from South America, have invaded via the West Indies in recent decades. Shiny cowbirds, which lay their eggs in the nests of other songbirds, may be as real a threat to the reproductive success of native North American species as they have been to the yellow-shouldered blackbird (*Agelaius xanthomus*) in Puerto Rico (Wiley 1985). Shiny cowbirds have been found as far north as Maine and as far west as Texas and Oklahoma.

Future Concerns

The North American avifauna has developed over millions of years, changing as climatic conditions altered habitats. New species evolved; others became extinct. Today, human influences are speeding extinction rates without any comparable increase in evolution of new species. Introducing aggressive exotic species often results in unforeseen problems, including extinction of native species.

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Non-native Animals on Public Lands

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Non-native plants and animals have become part of our surroundings, in cities, agricultural areas, and wildlands. While there are many beneficial purposes for non-native animals, such as for food and sport hunting and as agricultural animals, the introduction of some has had major negative economic consequences (Palmer 1899), and adverse effects on native wildlife, plants, and habitats. The British ecologist Charles Elton, in a major review of introduced species, described the increasing number of invasions as constituting "one of the great historical convulsions in the world's flora and fauna" (Elton 1958, p. 31).

Non-native species are significant problems on large areas of state and federal public lands, and areas set aside to protect native plant and animal communities are not immune to such harm. Science and conservation journals have devoted entire issues to the threats posed by non-native plants and animals in nature reserves (e.g., Usher et al. 1988). In a compilation of threats to U.S. national parks, non-native plants and animals were the most often reported threat, and were reported by the most areas; feral cats (*Felis catus*), feral dogs (*Canis familiaris*), and wild pigs (*Sus scrofa)* were the non-native animals cited most often (NPCA 1977). Non-native species present serious threats, but at the same time, coordinated efforts on public lands offer the best possibility for controlling some harmful non-native species, and protecting both native plant and animal communities and human interests and needs.

We compiled information on non-native animals on public and private land-management areas by conducting a mail survey to assess their occurrence and management status in land-management areas. Survey results represent contributions from 937 national parks, national forests, national wildlife refuges, Bureau of Land Management field areas, and state and private land-management areas. The results reflect those species that land managers considered of greatest concern, and their general distribution on public lands. Non-native invertebrate animals, particularly forest insects and agricultural pests, cause severe economic and environmental damage as well (OTA 1993), but were not the focus of this survey.

Distribution and Effects

The forests, parks, refuges, and other areas that responded to the surveys identified 205 non-native animal species as species of management concern. As a group, non-native mammals were most often reported by land managers as problem species, accounting for 60% (823 of 1,370) of the reports received (Table 1). Twenty-eight non-native mammal species were listed for the areas surveyed, with feral cats and dogs and wild pigs reported most often (Table 2). Feral cats and dogs are nearly ubiquitous (Figure) and are of concern because they prey on native birds and mammals (Van't Woudt

Table 1. Non-native species reported from U.S. national forests, parks, refuges, and other land-management areas. "Species introduced" is the total number of non-native species of each group that are known to have been brought into the United States (fish from Courtenay and Stauffer 1984; amphibians and reptiles from Smith and Kohler 1977; birds from Long 1981; mammals from Lever 1985). "Established" is the number of species that have established successful long-term populations. "Species reported" is the number of species noted in mail surveys sent to U.S. land-management areas, and "Number of reports" is the number of areas reporting each species.

	Fish	Amphibians	Reptiles	Birds	Mammals
Species introduced	104	27	67	119	40
Established	41	14	35	56	35
Species reported in this survey	40	3	4	19	28
Number of reports	272	24	6	245	823

Table 2. Non-native animal species most commonly reported in national forests, parks, and other U.S. land-management areas.

Name		No. of areas
Common	Scientific	
Cat (feral)	*Felis catus*	180
Dog (feral)	*Canis familiaris*	123
Pig	*Sus scrofa*	100
European starling	*Sturnus vulgaris*	93
Carp	*Cyprinus carpio*	56
Cow	*Bos taurus*	35
Horse	*Equus caballus*	31
Nutria	*Myocastor coypus*	29
Rainbow trout	*Oncorhynchus mykiss*	28
Burro	*Equus asinus*	25
Goat	*Capra hircus*	25
Brown trout	*Salmo trutta*	23
Brook trout	*Salvelinus fontinalis*	21
Red fox	*Vulpes vulpes*	11
Rock dove	*Columba livia*	28

1990). Wild pigs were reported primarily in the southeastern United States, California, and Hawaii; despite their status as game in most areas, they pose serious threats to native plant communities and rare plant species by their foraging and digging (Singer 1981; Stone and Loope 1987). Wild horses (*Equus caballus*) are primarily present in the western United States and on the barrier islands of the east coast. Although they may damage native vegetation, wild horses are generally protected as part of the historic scene.

After mammals, non-native fish were listed most often as problem non-native species. For all areas combined, we received 272 reports representing a total of 40 non-native fish species. Non-native trout (introduced to augment local fisheries) and common carp (*Cyprinus carpio*) were reported most. Introduced trout include species from other parts of the United States (e.g., eastern brook trout, *Salvelinus fontinalis*, introduced in many areas of the West) and species from other areas of the world (primarily European brown trout, *Salmo trutta*). Introduced trout may decimate susceptible native fish populations, lead to the loss of native varieties through interbreeding, and deplete amphibians and aquatic invertebrates in waters originally without fish (Taylor et al. 1984; Larson and Moore 1985). Most areas reporting problems or threats from non-native trout are in the western United States (Figure). Carp have been introduced in waters throughout much of the United States, but most areas reporting them as serious pests were wetland-management districts and wildlife refuges along the Mississippi, Missouri, and Columbia river systems.

We received 245 reports of non-native birds from survey respondents. Although many bird species have been introduced into the United States (Table 1), many failed to become established or remained restricted to areas where introduced. Only 19 species were reported as causing significant damage. European starling (*Sturnus vulgaris*) and rock dove (common pigeon, *Columba livia*) were reported most often, primarily in developed areas.

Only three non-native amphibian species and four non-native reptiles were reported. These species (e.g., marine toad, *Bufo marinus*) are primarily a problem in tropical and subtropical areas of southern Florida and Hawaii and some U.S. territories.

Seventy-three of the species identified in the surveys had been targeted for control or eradication. Feral cats were the subject of the greatest number of management projects (138 areas). Seventy-eight areas were conducting or had completed projects to control wild pigs, while 60 areas listed management for feral dogs, 41 for wild horses, 35 for cows (*Bos taurus*), and 35 for feral burros (*Equus asinus*).

Non-mammalian species were less often targets for control. Thirty-four areas, primarily U.S. Fish and Wildlife Service areas, listed control or eradication programs for carp. Other fish subject to control were introduced rainbow trout (*Oncorhynchus mykiss*; 22 areas) and brook trout (20 areas) in streams in western North America. Fewer projects were listed for birds. European starlings were the target of most controls (15 areas). A few areas listed control projects for non-native invertebrates. Most common were fire ants (*Solenopsis* spp., 14 areas) and gypsy moths (*Lymantria dispar;* 9 areas).

This survey highlights widespread and serious concerns about the effects of introduced species on native plant and animal communities. Geographically, this was true for areas across most of the United States except Alaska, where survey respondents generally reported few problems with non-native species, possibly because of the extreme climate of that area. Even there, however, non-native species can be a serious threat in local areas; some nesting waterfowl and seabirds on island wildlife refuges are severely affected by predation from introduced Arctic foxes (*Alopex lagopus*).

Some of the greatest adverse impacts of non-native species have been in freshwater communities and on islands. Introduced fish have caused calamitous changes in the Great Lakes, decimating both the natural community of the lakes and the commercial fishery that depends on these inland seas (Lawrie 1970; Eck and Wells 1987). Adverse effects of introduced fish, especially predaceous species, on native fish, amphibians, and invertebrates are a recurrent pattern (Taylor et al. 1984; Moyle 1986). Introduced brown trout, in particular, are serious predators on native salmonids in the United States. In spite of their small size, introduced western mosquitofish (*Gambusia affinis*) may eliminate other small, native fishes through competition or predation; they may also prey heavily on the young of food and game fish and also on aquatic amphibian larvae (Meffe et al. 1983).

Non-native species introduced to islands have caused the greatest harm to terrestrial plant and animal communities. Areas specifically responding to our surveys included the national seashores on the barrier islands of the east coast and Gulf of Mexico, the National Park Service on the California Channel Islands, and national parks and wildlife refuges on the Hawaiian Islands. It is generally considered that long-isolated island plants and animals are poorly adapted to cope with introduced predators, competitors, and disease organisms, and all of these island areas have suffered serious damage from

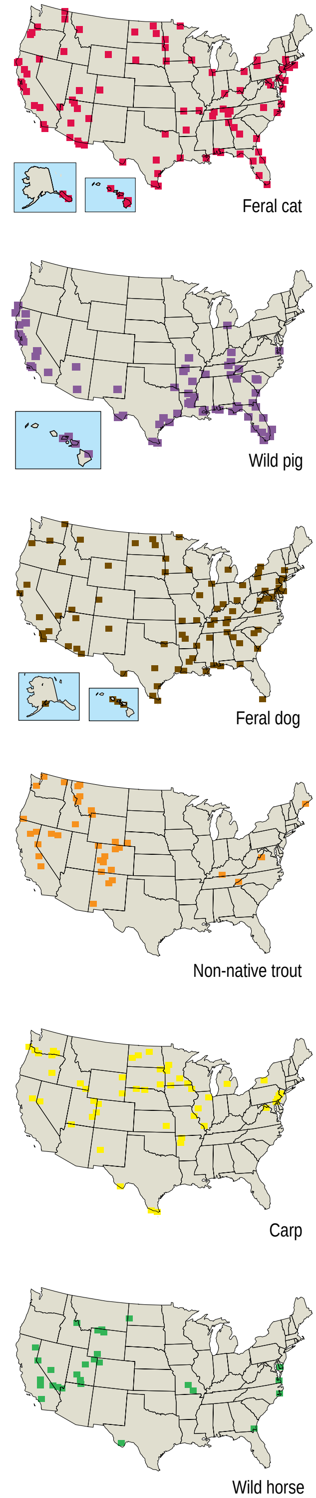

Figure. Distribution of several non-native animal species on public lands as reported by land managers responding to mail surveys: feral cat, wild pig, feral dog, non-native trout, carp, and wild horse.

introduced herbivores such as goats (*Capra hircus*), pigs, and Old World rabbits (*Oryctolagus cuniculus*), and introduced predators such as feral cats, rats, and mongooses (*Herpestes auropunctatus*; Stone 1985; Brockie et al. 1988). At the same time, these island areas have had some of the greatest success at controlling and managing non-native species. Feral goats, pigs, rabbits, and cats have been eliminated from some of the Channel Islands, allowing native plant and animal communities to begin to recover, and Hawaiian parks and refuges have successfully protected parts of their unique flora and fauna through aggressive and innovative control and exclusion measures against non-natives (Stone and Loope 1987).

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Exotic Species in the Great Lakes

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Global transfer of exotic organisms is one of the most pervasive and perhaps least recognized effects of humans on aquatic ecosystems of the world. Such transfers to new environments may lead to loss of species diversity and the extensive alteration of the native community. These changes, in turn, may have broad economic and social effects on the human communities that rely on the system for food, water, or recreation. Here we describe the exotic aquatic species that have become established in the Great Lakes and discuss their entry mechanisms or routes, the timeline of introduction, their geographic origins or sources, and their effects on the ecosystem of the Great Lakes. A recent review (Mills et al. 1993) provides the basis for much of this report.

Introductions of Species

Since the early 1800's, at least 139 new aquatic organisms have become established in the Great Lakes (Fig. 1); most are aquatic or wetland plants (42%), fishes (18%), and algae (17%). Introduced species of mollusks, oligochaetes, crustaceans, flatworms, bryozoans, cnidarians, and disease pathogens combined represent 22% of the total. All entered the Great Lakes basin by major mechanisms or routes (Fig. 2) including shipping (41 exotic species); unintentional releases (40 new species); ship or barge canals, along railroads or highways, or deliberate releases (17 species); unknown entry vectors (14 species); and multiple entry mechanisms (27 species).

The rate of introduction of exotic species increased markedly since the 1800's, as human activity in the Great Lakes basin increased. Almost one-third of the introductions to the Great Lakes were reported in the past 30 years. The first introductions of aquatic plants occurred when ships discharged solid ballast in the late 1800's. The opening of the St. Lawrence Seaway in 1959 greatly increased the number of ocean-going vessels entering the Great Lakes and dramatically increased the entry of exotic species by ships. Deliberate releases declined after the 1800's, and entry by canal increased slightly through 1959; entry by railroad and highway occurred mostly in the 1800's, and unintentional releases were consistently high since the late 1800's.

Origins of Introduced Species

Although most exotic species established in the Great Lakes are native to Eurasia (55%) and the Atlantic coast (13%), Great Lakes populations of many of these exotic species may have been established from sources outside their original native range. Purple loosestrife (*Lythrum salicaria*), Eurasian watermilfoil (*Myriophyllum spicatum*), and the Asiatic clam (*Corbicula fluminea*) are examples of Eurasian organisms that invaded the Great Lakes from source populations established outside their native ranges. Invading Atlantic coast species, such as sea lamprey (*Petromyzon marinus*) and white perch (*Morone americana*) probably entered through the Erie and Welland canals. Pacific salmon (*Oncorhynchus* spp.), rainbow trout (*O. mykiss*), brown trout (*Salmo trutta*), alewife (*Alosa pseudoharengus*), and rainbow smelt (*Osmerus mordax*) are examples of species that were introduced directly into the Great Lakes basin from populations in their original native ranges.

Effects of Introductions

The ecological and economic effects of the introduced fish species have been large. Of the 25 introduced fish species established in the Great Lakes, nearly half have had substantial effects. The extension of the range of the sea lamprey since the 1830's contributed to the decline of several fish species and severely damaged the sport and commercial fisheries of the Great Lakes. Millions of dollars are spent annually on sea lamprey control. The lake trout was the major predator species in the four lower Great Lakes, and its extermination by the sea lamprey allowed the alewife to move quickly through the lakes and experience almost unrestrained population growth. This growth was followed by massive die-offs of alewives, which polluted shorelines and blocked the intake pipes of water treatment plants and other industries. The alewife probably also suppressed native coregonines (*Coregonus* spp.), yellow perch (*Perca flavescens*), emerald shiner (*Notropis atherinoides*), and rainbow smelt. Eventually the alewife became an important prey for trout and salmon.

The ruffe (*Gymnocephalus cernuus*), a small, perchlike fish, reached the St. Louis River estuary in Lake Superior in ballast water in the early to mid-1980's. Ruffe abundance increased rapidly and in 1993, 61% (by number) of the fish caught in 440 bottom-trawl tows in the estuary were ruffe (J.H. Selgeby, National Biological Service, personal communication). The ruffe is spreading to other parts of the lake and has the potential to occupy at least 6.6 million ha (16.3 million acres) of Great Lakes' habitat that is suitable for use by native percid fishes, including the economically important walleye (*Stizostedion vitreum*) and yellow perch (Edsall et al. 1993). The effect of ruffe on native Great Lakes percids has not been demonstrated, but yellow perch numbers in the St. Louis River estuary declined markedly as ruffe abundance increased. There is concern that the ruffe has the potential to adversely affect percid abundance in other areas of the Great Lakes.

The common carp (*Cyprinus carpio*) was stocked in the 1870's, but it never became popular and by the 1890's was considered a problem because of its negative effects on more favored fish species and on waterfowl habitat. The stockings of Pacific salmon and rainbow and brown trout had profound and permanent ecological effects on the fish fauna through competition and predation. These salmonids now support a major element of the fishery in the Great Lakes, valued at more than $6 billion annually (GLFC 1992).

Of the fish disease pathogens introduced into the Great Lakes, *Glugea hertwigi*, a protozoan, caused extensive mortality in rainbow smelt in Lakes Erie and Ontario in the 1960's

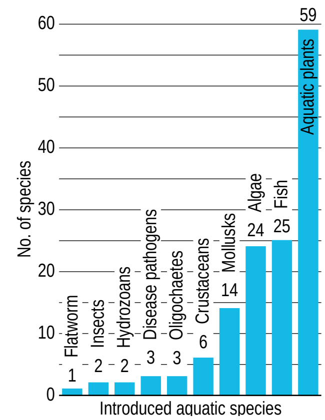

Fig. 1. Introduced aquatic species established in the Great Lakes. The number of species in each category is given above the bars.

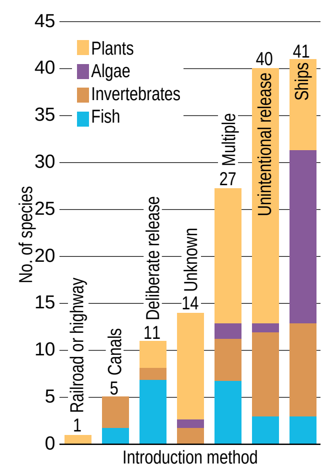

Fig. 2. Entry mechanisms or routes of exotic species established in the Great Lakes. The number of species in each category is given above the bars.

Courtesy T.A. Edsall

The introduced ruffe *(Gymnocephalus cernuus).*

and 1970's. A second pathogen, bacterial kidney disease, has been implicated in the massive mortalities of Pacific salmon in Lake Michigan in recent years (MDNR 1992). Two other introduced pathogens cause salmon whirling disease and furunculosis, but they occur mainly in fish hatcheries where crowding makes fish vulnerable to outbreaks of disease.

The arrival of the zebra mussel (*Dreissena polymorpha*) in Lake Erie in 1986 (Leach 1992) set the stage for long-term changes in pelagic and benthic communities in the Great Lakes and in the economic and social future of lake users. The zebra mussel may cause substantial changes in the food chain, resulting in a probable reduction in the overall production of fish in the Great Lakes. Zebra mussels also foul private vessels and structures, and nautical and littoral structures, including water intakes, in the Great Lakes. The zebra mussel has spread to southern Ontario in Canada; its westward range extension includes the Mississippi River and some of its tributaries from the river's headwaters near St. Paul, Minnesota, to its mouth at New Orleans, Louisiana. Negative ecological, economic, and societal effects are expected from these and future range expansions.

Introduced plant species outnumber all other groups of introduced organisms, but the effects of only a few of these are known. Purple loosestrife has spread throughout the Great Lakes basin and is replacing the cattail (*Typha latifolia*) and other wetland native plants. Purple loosestrife has no food value for wildlife and is making wetlands less suitable as wildlife habitat. Eurasian watermilfoil has also had a substantial effect in lakes in the Great Lakes basin. Massive beds of the plant often make boating and swimming impossible and reduce fish and invertebrate populations. Some introduced species of algae have become dominant members of the algal community of the Great Lakes. Their ecological impacts are generally unknown, but one, *Stephanodiscus binderanus*, has caused water-quality problems on several occasions.

The ecological effects of the introduced crustaceans, oligochaetes, bryozoans, cnidarians, and flatworms are largely unknown. Historically, the ecological and economic risks associated with these groups have not been as high as those posed by other plants and animals. The recently introduced spiny water flea (*Bythotrephes cederstroemi*), a predatory zooplankter, has rapidly expanded in the Great Lakes. Its ecological effect is unknown, but its establishment in Lake Michigan coincided with observed changes in the zooplankton community characteristic of those caused by an invertebrate predator.

Conclusions

The ecological, social, and economic effects of exotic species in the Great Lakes continue to be enormous. Serious effects have been documented for only a fraction of the species introduced into the Great Lakes. However, most introduced species have not been thoroughly studied to determine their effects on the ecosystem. Introduced species exist at almost every level in the food chain, and their effects must certainly pervade the entire aquatic community of the Great Lakes. We believe that as long as human-mediated transfer mechanisms persist and habitat alterations that stress native aquatic communities are allowed to occur, the Great Lakes ecosystem will also be at substantial risk from new, undesirable, exotic species.

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Zebra Mussels in Southwestern Lake Michigan

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The zebra mussel (*Dreissena polymorpha*) is a European species that was accidentally introduced into North America. It has had a tremendous impact on freshwater ecosystems of the United States and Canada. Since the zebra mussel was first discovered in Lake St. Clair in 1988, it has spread to each of the Great Lakes and to the major river systems of central and eastern United States. Communities along the affected lakes and rivers rely on these waters for drinking, industrial water supplies, transportation, commercial fishing and shelling, and recreation. Rapidly expanding populations of zebra mussels could ultimately affect many of these activities, in addition to changing the structure of the ecosystem.

By firmly attaching to hard surfaces, zebra mussels have clogged water-intake pipes and fouled hard-shelled animals such as clams and snails. In addition, zebra mussels have reduced plankton populations as colonies of mussels filter large volumes of water for food (e.g., Holland 1993), potentially depleting food resources of larval and planktivorous fishes such as smelt, chub, and alewife (*Alosa pseudoharengus*). Transfer of suspended material to the lake bottom in mussel waste products also leads to increased water clarity (Reeders et al. 1992) and increased growth of aquatic plants, a phenomenon already observed in some of the shallower harbors of Chicago. Although clear water is often considered aesthetically pleasing, this clarity indicates that drastic changes have occurred at the base of the food web and that energy flow through the ecosystem has been altered.

The first live zebra mussel was discovered in Lake Michigan near Chicago in 1989. We documented the subsequent establishment of the zebra mussel in southern Lake Michigan by monitoring larval and adult zebra mussels in 1991-93. Monitoring was conducted primarily along the Illinois and Indiana shorelines; limited sampling occurred along the southern Wisconsin shoreline. We also quantified the initial effects of the invasion on water clarity and native fauna.

Zebra Mussel Densities

Larval zebra mussels were present at all sampling locations during 1991-93; however, the number of sampling locations decreased from 8 to 3 over the 3 years. Peak numbers were collected each year at Burns Harbor, Indiana, where the highest average density was 37,044 veligers/m^3 (1,049/ft^3) in 1991; 74,493/m^3 (2,109/ft^3) in 1992; and 42,099/m^3 (1,192/ft^3) in 1993.

Attached zebra mussels were found in quite low numbers (less than 150/m^2 or 14/ft^2) in 1991 at one Wisconsin and four Illinois locations sampled by divers. The maximum density in 1991 (up to 2,389/m^2 or 222/ft^2) was recorded on concrete blocks in the intake channel of an Indiana power plant inaccessible to divers. By 1992, sampling at 2 Wisconsin and 4 Illinois sites revealed that the population had exploded, with a *minimum* average density of 57,115/m^2

Courtesy D.W. Schlosser, NBS

Zebra mussel (*Dreissena polymorpha*) on fragile papershell mussel (*Leptodea fragilis*).

Invasion of the Zebra Mussel in the United States

by
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Passage of the Nonindigenous Aquatic Nuisance Prevention and Control Act of 1990 called for a national program to control and reduce the risk of further introductions of nonindigenous aquatic nuisance species. This legislation specifically addressed the non-native zebra mussel (*Dreissena polymorpha*), which is expected to affect two-thirds of the nation's waterways.

The zebra mussel, a European species, was first discovered in Lake St. Clair in June 1988 and is now well established in North America. Zebra mussel introductions through ballast water may be responsible for many other introductions to the Great Lakes as well.

Aside from economic impacts, there could also be severe biological impacts. Plankton populations are directly affected by zebra mussels because of the tremendous filtering capacity of large mussel colonies; this could potentially shift system energetics and reduce available food resources for higher organisms. Biologists in the Great Lakes region believe that zebra mussels have already had an effect on the ecology of Lake St. Clair (Griffiths 1993); increased water clarity there potentially could cause a shift in the fish species composition. There has also been a detrimental effect on native mussel populations in Lake Erie since the arrival of zebra mussels (Masteller and Schloesser 1991). Native freshwater mussels are affected when zebra mussel larvae settle and attach on native mussels, covering them so completely that they can no longer carry out life processes. In addition, zebra mussels reduce the amount of food and possibly oxygen available to native mussels.

One important part of the nonindigenous program is to monitor the zebra mussel's distribution and provide technical assistance to other federal agencies, states, and the private sector. The National Biological Service's Southeastern Biological Science Center (SBSC) in Gainesville, Florida, monitors the zebra mussel as part of this program. By using the zebra mussel as a prototype species, personnel at SBSC also began developing a national geographic information system (GIS) to organize a coherent set of nonindigenous aquatic species data.

Federal, state, and private cooperators supplied us with information, resulting in the most complete digital data set of zebra mussel sightings in North America (Boydstun and Benson 1992). The locations of sightings were then entered into a data base. Since July 1991, between the United States and Canada we have collected more than 1,000 records of zebra mussel occurrences going back to their discovery in 1988 in Lake St. Clair.

Types of Observations

Zebra mussels are observed and collected by artificial substrate samplers, plankton nets, and inspection of pipes and water intakes. In the Great Lakes pipes and water intakes at power plants, water-treatment facilities, and various industries pump lake water into their plants. Zebra mussels clog these water pipelines, causing serious mechanical problems. The U.S. Coast Guard found zebra mussels on navigational buoys in the Great Lakes during routine inspections; these buoys now serve as an artificial substrate sampler, giving us hundreds of records each winter. Zebra mussels have also been collected inadvertently while sampling for fish when using gill nets or when collecting native mussels. The incidental finds account for many important sightings in newly expanded areas.

Range Expansion

Since the first zebra mussel was sighted in 1988 (Fig. 1), the species quickly colonized regions in all five Great Lakes by 1990. Currently, they have been reported in the waterways of 19 states and 2 Canadian provinces (Fig. 2). They are established in the Great Lakes and the following rivers: Mississippi, Arkansas, Illinois, Ohio, Tennessee, Cumberland, Hudson, Susquehanna, Ottawa, Niagara, Mohawk, Genesee, Kanawha, and St. Lawrence. Established colonies exist throughout the lower Great Lakes (Erie, Ontario, and St. Clair) wherever there is suitable habitat. Lake Huron has populations in Saginaw Bay and at the southern end of the lake where it flows into the St. Clair River. There are also a few isolated populations around the lake and in the Georgian Bay area. Zebra mussels are abundant in most of the southern portion of Lake Michigan's shoreline from Sheboygan, Wisconsin, to Frankfort, Michigan. The northern portion of the lake has populations in Green Bay, Traverse Bay, and in the lake at Escanaba and St. Ignace, Michigan. Zebra mussels have also been found in 11 inland lakes in Michigan. Lake Superior is the only Great Lake where zebra mussels are not spreading quickly. Since the first sightings in Duluth Harbor in October 1989, they have been found only in Thunder Bay (Canada), Sault Ste. Marie, and Marquette, Michigan.

The first sighting in the Mississippi River was in Alton, Illinois, on 10 September 1991. Two days later a single zebra mussel was found about 764 km (475 mi) upstream at La Crosse, Wisconsin. In January 1992, mussels were found at Clarksville, Missouri; Oquawka, Illinois; and Genoa, Wisconsin. In July 1992, mussels were reported near Winona, Minnesota. By early 1993 (Fig. 3), almost every lock and dam in the Upper Mississippi River north of Dubuque, Iowa, had zebra mussels. The Lower Mississippi River was colonized more recently in the later part of 1992 and early 1993. Mussels were collected in the river at Greenville and Vicksburg, Mississippi, in 1992. By the end of June 1993, zebra mussels were collected in Louisiana at Shaw, Lettsworth, St. Francisville, New Orleans, and Berwick.

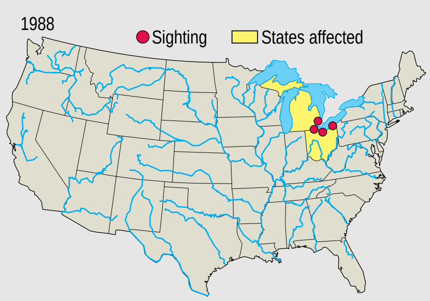

Fig. 1. States with zebra mussel sightings in inland or adjacent waters, 1988. In 1989, they spread to Lake Superior, Lake Michigan, and Lake Ontario (National Biological Service, unpublished data).

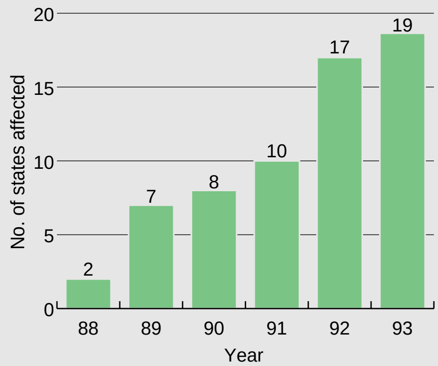

Fig. 2. Numbers of states affected by zebra mussels since their arrival in the United States in the mid-1980's.

Vectors

It is important to be aware of the spread of nonindigenous species, especially ones with the potential to be an ecological menace such as the zebra mussel. The natural means of dispersal is larval drift downstream. Aside from natural mechanisms, canals and barge traffic in navigable rivers are suspected as major vectors for dispersal. In April 1992, a barge dry-docked for repairs at Hartford, Illinois, had more than 1,000 zebra mussels attached to a section of exposed hull (Keevin et al. 1992). The total number of zebra mussels on the entire hull could not be determined. The barge's log book showed that it had traveled 20,558 km (12,777 mi) up and down the Mississippi River from Minnesota to Louisiana in just over 1 year before dry-docking. This documented long-distance transport of live mussels gives credibility to the assumption that barge traffic has been a primary dispersal mechanism in navigable waters. Zebra mussels can also be dispersed overland, especially by human activities such as recreational boating. Dead zebra mussels from Lake Erie were found on a boat trailer entering California (D. Peterson, California Department of Water Resources, personal communication).

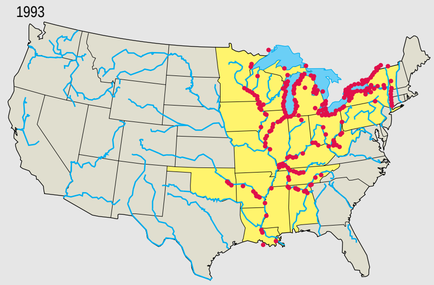

Fig. 3. States with zebra mussel sightings in inland or adjacent waters in 1993. The range has extended west of the Mississippi River into Oklahoma by way of the Arkansas River (National Biological Service, unpublished data).

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(5,306/ft^2) near Glencoe, Illinois. The *maximum* average density in 1992 was 267,885/m^2 (24,885/ft^2) at a Waukegan site that 1 year previously had only 25 mussels/m^2 (2/ft^2) (Marsden et al. 1993). Densities at two Illinois locations remained high in 1993, with average densities of 224,428/m^2 (20,858/ft^2) at Waukegan and 52,428/m^2 (4,870/ft^2) at Lake Forest.

High reproductive success during 1991 was clearly responsible for the huge increase in the number of attached mussels during 1992. It is interesting that although 1992 levels of reproduction were generally twice as high as in 1991, the population increase did not continue in 1993 at the two locations sampled.

Water Clarity

Water visibility (using a secchi disk) increased from a maximum depth of 4 m (13 ft) in 1990, to 6 m (20 ft) in 1991, to 10 m (33 ft) in 1992. Water remained clear in 1993, with a maximum depth at disappearance of 9.5 m (31 ft). At the site for which data are most consistently available (Waukegan), minimum water visibility measurements during 1991-93 were higher than any measured values during 1990. This trend should be interpreted with caution given the natural variability in water clarity values. The data suggest, however, that the water clarity of southern Lake Michigan may be increasing due to colonization of the lake by massive numbers of zebra mussels. This trend has been documented in other recently colonized lakes, such as Lake Erie (Leach 1992).

Impacts on Snails

Most native snails we collected were colonized by one or more zebra mussels. *Stagnicola* was the most common genus collected in nonquantitative samples. In 1991, 72% of these snails had attached zebra mussels, with an average of 1.6 mussels per snail. By 1992, 99% of *Stagnicola* were fouled, with the average number increasing to 3.7 zebra mussels per individual snail. *Elimia* snails dominated the quantitative samples from rocky areas. In 1992, 99% of 94 *Elimia* were fouled with mussels; in 1993 divers failed to find any live *Elimia* at the Waukegan reef.

Conclusions

In the Great Lakes and associated river systems, populations of native clams are threatened because of the colonization of their shells with massive numbers of zebra mussels (Mackie 1991). Our data indicate that snails are also being used as substrate for mussel attachment in Lake Michigan. As grazers, snails are an important part of the bottom community. They are also a source of food for fishes such as yellow perch (*Perca flavescens*), sunfish, and whitefish (Scott and Crossman 1973). Given the limited knowledge of the role of snails in Lake Michigan and other large lakes, it is not possible to fully anticipate the effects of reduced or decimated snail populations.

The rapid increase in zebra mussel densities we observed in the open waters of the lake was reflected in their colonization of municipal and industrial water-intake pipes. In 1991 and 1992 facilities drawing raw water from Lake Michigan began treatment programs to reduce infestation of intake pipes. The cost of retrofitting plants in Chicago and northern Illinois shoreline communities had totaled $1,778,000 by 1992 (Nelson 1992). This value does not include chemical costs, or increased personnel costs as workers dealt with mussel-related problems. In addition to economic costs of retrofitting and chemical treatments, Lake Michigan has an increased ecological risk of accidental chemical spills or leakages.

Zebra mussels also affect the aesthetic and recreational value of the lake. Boat owners are concerned about zebra mussels fouling boat hulls and engine cooling systems, and windrows of broken shells have begun to appear along Lake Michigan beaches.

The economic impact of zebra mussels is not limited to industrial and recreational interests, however. Native clams from the Illinois River are shipped to Japan for use in the cultured pearl industry; in 1991 the value of this resource was $1.4 million annually. The infestation of clams by zebra mussels has increased dramatically, resulting in significant clam mortality. Commercial shelling on the Illinois River was recently banned, following a drop in harvest from over 454,000 kg (1 million lb) in 1991 to 67,646 kg (149,000 lb) in 1993 (Don Duffert, Illinois Department of Conservation, personal communication).

Zebra mussels are a permanent addition to the Lake Michigan ecosystem and connected waters. Chemical and mechanical controls for zebra mussels are only useful in localized areas such as intake pipes and other artificial structures, but not in the open waters of the lake. Ultimately, zebra mussel populations will exceed the capacity of the environment to support them, after which their numbers will likely decline. Native predators such as freshwater drum (*Aplodinotus grunniens*), diving ducks, and crayfish may also keep mussel populations in check in some areas. The adverse effects of zebra mussels on human activities and native aquatic species will never be totally eliminated, but eventually they may become a more tolerable nuisance.

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Africanized Bees in North America

by

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The honeybee genus *Apis* likely has the greatest breadth of pollen diet of any insect and, because of its human-caused cosmopolitan distribution, the species directly affects the reproductive biology of about 25% of the world's flowering plants (Schmalzel 1980; Buchmann et al. 1992). This situation has profound consequences for agribusiness, native plants and animals, and ecosystems. In 1956, bee geneticist Warwick E. Kerr imported queen bees of an African race (*Apis mellifera scutellata*) into Brazil to breed a more productive honeybee that was better adapted to the Neotropical climate and vegetation (Kerr 1967). The following year, 26 of Kerr's Africanized honeybee queens were inadvertently released into the surrounding forest (Winston 1987). Since then, the Africanized hybrids have been expanding their range northward, with an average rate of between 330 and 500 km (200 and 300 mi) each year (Fig. 1).

The first U.S. Africanized honeybee colony was reported in October 1990, at Hidalgo, Texas, along the international boundary. By fall 1993, Africanized honeybees (AHBs) had extended their territory north and west into numerous counties of Arizona, New Mexico, and Texas (Fig. 2). Since the first U.S. AHB swarm was detected, the rate of spread has accelerated to over 600 km (375 mi) per year in the southwestern United States (Guzman-Novoa and Page 1994).

European honeybees (EHBs) were introduced into North America as early as the 16th century by Spanish conquistadors and missionaries (Brand 1988). Today, one of the three most common subspecies or races of the EHB, the Italian honeybee (*A.m. ligustica*), is nearly pandemic throughout North America because of its popularity with professional and hobbyist beekeepers. As a consequence, these non-native bees have become naturalized and have been a part of the North American arthropod biota for about 3,500 bee generations, or at least the past

Courtesy J.O. Schmidt, USDA

Africanized honeybees swarm outside a trap in Costa Rica.

200 years (Buchmann et al. 1992). European honeybees are commonly seen visiting agricultural food crops, cultivated flowers, and roadside wildflowers to gather nectar and pollen. They are even common in areas far from human population centers. These bees are also the preferred, "managed" pollinator for over 100 U.S. agricultural crops (e.g., fruits, vegetables, and some nuts), most of which depend on or benefit from insect pollination. The value of these pollination services by EHBs is estimated at \$5-\$10 billion annually in the United States (Southwick and Southwick 1992).

Africanized and European honeybees represent divergent subspecies within the *mellifera* species of the genus *Apis*. Both have nearly the same biochemistry, morphology, genetics, diet, and reproductive and other behaviors. Their diet includes pollen and spores from most seed plants. Both EHBs and AHBs are social bees living in perennial colonies. They are active on most days collecting nectar, water, pollen, and plant resins for their subsistence. These honeybees "hoard" excess honey as energy-rich carbohydrate reserves in hexagonal wax combs. Energy from honey consumption partially supports brood-rearing and, most importantly, supplies the energy necessary for foraging flights by thousands of adult worker bees.

Fig. 1. Migration of Africanized honeybees.

Africanized and European honeybees exhibit different foraging strategies (largely tropical versus temperate attributes). Africanized honeybee colonies in Africa, and now in much of the Neotropics, are attuned to finding and exploiting isolated mass-flowering tropical trees, and also use pollen and nectar from the nocturnal flowers of bat-pollinated flowering plants. Some tropical *Apis* species even migrate to follow nectar and pollen flows across the floral landscape. Consequently, these bees depend on increased colony mobility (reproductive swarming and abandoning the hive) as behavioral responses to seasonal floral richness or dearths. EHBs are better at hoarding vast amounts of honey and surviving long, cold winters.

Although preliminary evidence for behavioral differences between the two races have been documented in the Neotropics (French Guiana, Venezuela, Panama; *see* reviews by Taylor 1977; Seeley 1985; Roubik 1989), the behavioral ecology of AHBs and their interactions with EHBs and thousands of species of native U.S. bees remain largely unknown. Africanized honeybees have slightly shorter developmental times than do European bees, enabling them to produce more bees per unit time compared with EHBs. Africanized bees will also accept smaller cavities to nest in than European bees. This behavior increases potential competition for nesting sites with birds and other animals and also increases the potential for greater numbers of honeybee colonies in an area. Africanized honeybees commonly abandon their hives, often 15%-30% annually or even much greater in some localities. Absconding colonies may travel as far as 170 km (about 100 mi) before selecting a new nesting site (USDA 1994). Thus they have been able to rapidly colonize new areas in the Neotropics.

The most often-discussed characteristic separating the two races is the AHBs' propensity to vigorously defend their colony and nest site. Although all honeybees respond to threats to their colonies, AHBs respond more quickly and in much greater numbers than do EHBs. In comparison to EHBs, greater numbers of AHBs will pursue intruders for much greater distances to defend their colonies. Recent research reported that 3 to 4 times as many AHBs responded and left 8 to 10 times more stings in a black leather measuring target in stinging experiments (USDA 1994).

Biochemical comparisons of AHB and EHB venoms indicate they are nearly identical. Nineteen stings per 1 kg (2.2 lb) of human victim body weight is the predicted median lethal dose (Schumacher et al. 1992). Massive stinging incidents by AHBs are more likely to result in toxic envenomation. Reported 1993 stinging incidents in Mexico have involved more than 60 human fatalities (one death per 1.4 million). From 1988 to 1992, the Mexican national African Bee Program eliminated 117,000 AHB swarms in densely populated urban areas (Guzman-Novoa and Page 1994). To date, the worst U.S. stinging incident occurred in July 1992, when a 44-year-old man mowing his lawn experienced a massive bee attack resulting in 800-1,000 stings (McKenna 1992).

Ecological Implications

Competition among nectar- and pollen-feeding invertebrate and vertebrate pollinators, resource partitioning, insect and plant community interactions, and ecosystem processes are affected by introduced EHBs and AHBs, with important short- and long-term ecological and perhaps evolutionary consequences. The influence of exotic honeybees on individual species or communities of native tropical (or temperate) plants or animals can only have one of three outcomes: the native species will suffer, benefit, or remain more or less unaffected. The key to understanding these seemingly obvious outcomes is, however, based on obtaining sufficient information to delineate the very complex short- and long-term competitive dynamics between introduced bees, native bees and pollinators, and native plants in diverse, interacting, natural communities.

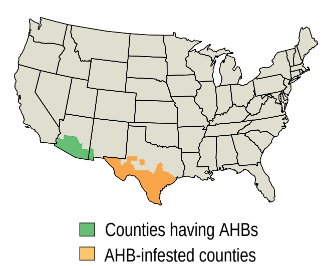

Fig. 2. Confirmed presence of Africanized honeybees in (colored) counties of Arizona, New Mexico, and Texas, January 15, 1994.

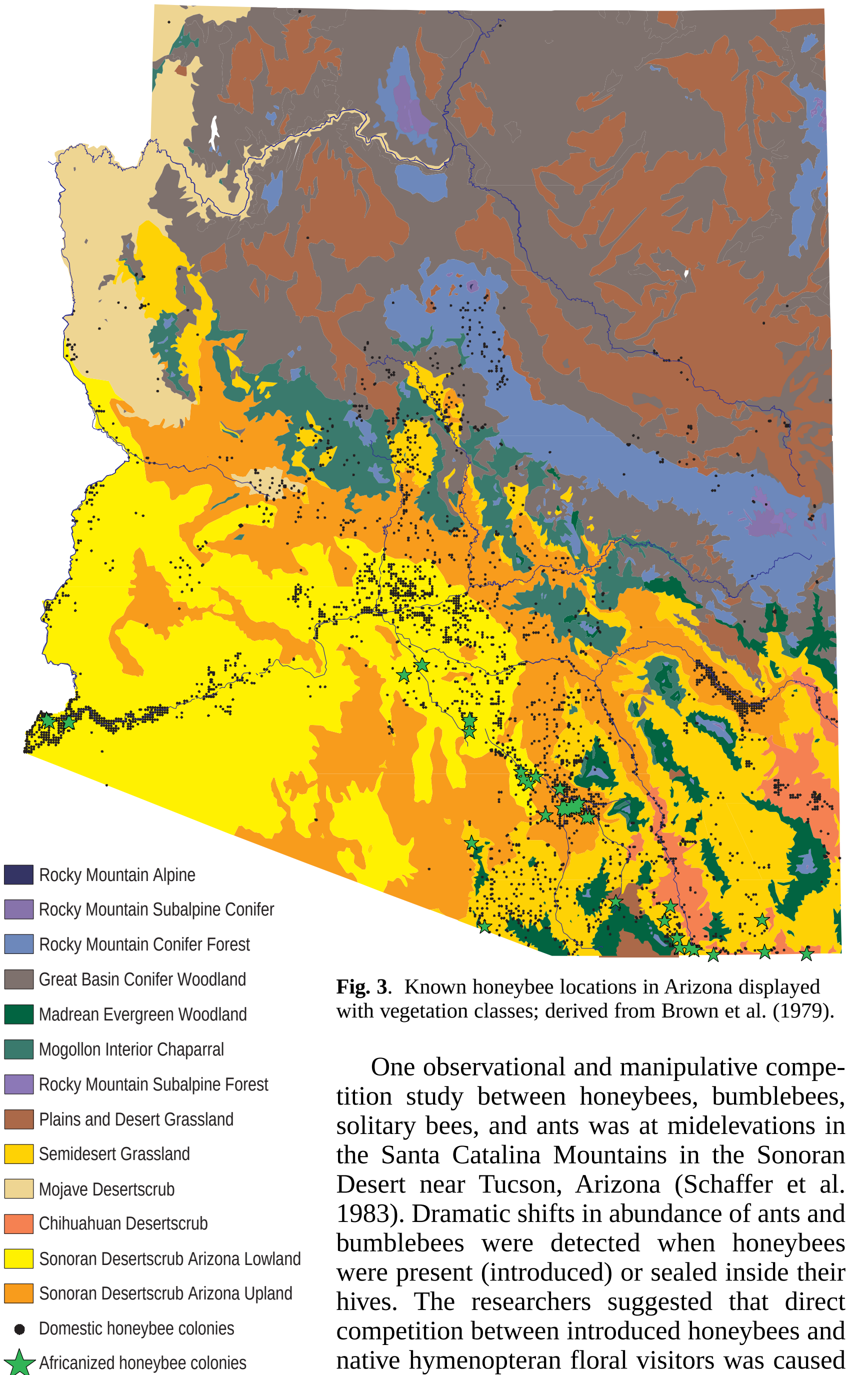

Fig. 3. Known honeybee locations in Arizona displayed with vegetation classes; derived from Brown et al. (1979).

One observational and manipulative competition study between honeybees, bumblebees, solitary bees, and ants was at midelevations in the Santa Catalina Mountains in the Sonoran Desert near Tucson, Arizona (Schaffer et al. 1983). Dramatic shifts in abundance of ants and bumblebees were detected when honeybees were present (introduced) or sealed inside their hives. The researchers suggested that direct competition between introduced honeybees and native hymenopteran floral visitors was caused by honeybees numerically dominating the site. Initial evidence seems to indicate that honeybees seek out and preempt the most profitable habitats and partially exclude native bees indirectly by rapidly reducing the standing crop of plant nectar and pollen (*Agave* in this study).

Both species of non-native bees forage vast expanses of territory containing native and non-native floral resources. Estimates of the amount of terrain foraged annually by an average-sized honeybee colony in New York hardwood forests (Visscher and Seeley 1982) are 80-100 km^2 (30-40 mi^2). Forage area estimates for AHB colonies living in lowland Panamanian rain forests (Roubik 1989) are 200-300 km^2 (75-115 mi^2), although 90% of these foraging flights are completed within 5 km (3 mi) of the nest (Visscher and Seeley 1982). Even given this restrictive caveat, the amount of "bee pasture" grazed by these aerial herbivores is immense.

In studying honeybee colonies foraging in temperate forests in New York State, Visscher and Seeley (1982) found that these cold-hardy EHB colonies amassed 15-30 kg (33-66 lb) of pollen and 60-80 kg (132-176 lb) of honey each year. To collect this amount of food, a colony must dispatch tens of thousands of foragers on many millions of foraging bouts with the bees flying 20-30 million km (12-19 million mi) overall. Similar studies of AHBs in Panama (Roubik 1989) determined that AHBs placed more emphasis on pollen collection. The Sonoran Desert of northern Mexico and southern Arizona is perhaps one of the richest areas in the world in floral resources because of the relative high plant diversity and the many fair-weather days for worker-bee foraging.

Many important nectar- and pollen-producing plants visited by AHBs bloom at night and are pollinated by bats. Africanized honeybees find and exploit these rich flowers at first light, and we predict that saguaros and other columnar cacti will be heavily used as food plants for AHBs in Arizona. Early Arizona data for AHB colonies illustrate that most AHB colonies have been found in the subtropical climate zones in Sonoran desertscrub.

Determining which plants are used primarily for nectar versus pollen, or both, depends on direct observations of bees on flowers or indirectly by identifying pollen grains in stored nest samples of honey. In Panama, Roubik (1989) found that AHB colonies harvested pollen from at least 142-204 flowering plant species in a forest containing about 800-1,000 species. European honeybees collected pollen or nectar from about 185 plant species from a secondary forest and agricultural area in Mexico (Villanueva 1984). These studies suggest that honeybees are using about 25% of the local flora, but intensively use far fewer species at any given time (Roubik 1989). In Arizona EHBs will often harvest pollen from more than 60 species annually, but of these, only 10-15 are harvested heavily and consistently from year to year (Buchmann et al. 1992). Because of their pollen herbivory and reproductive contact with so many plants, there can be serious long-term ecological and evolutionary consequences of these interactions that we simply do not yet understand.

Ecological Monitoring

Although we have made a case for potential serious, competitive displacement of food resources by honeybees to the exclusion of some native bees and pollinators, there is a little-appreciated yet unique ecological application for using EHB colonies (*A. mellifera*) as short- and long-term local and regional monitoring devices of vegetation diversity, plant productivity, flowering phenology, precipitation, climate, and general ecosystem health. No expensive equipment is required since the bees do all the "fieldwork." In addition, floral changes in landscapes can be determined from the rich "fossilized" source of pollen dietary information in old, dark brood combs or in 75- to 100-year-old "debris middens" in the Sonoran Desert (Buchmann et al. 1992). Long-term records (some spanning decades) for certain beekeeping locations are invaluable aids to beekeepers, ecologists, and resource managers for ecological evaluation and monitoring.

To validate any AHB range-expansion prediction or to measure potential effects on native pollinators or ecosystem components, we must monitor the bees and evaluate habitats on national and local scales. Information must be collected, integrated, and shared by researchers, individuals, and agencies. Public-and-private-sector partnerships have been developed to exchange AHB information and develop monitoring protocols.

Researchers use geographic information systems (GIS) and global positioning systems (GPS) technologies to track the locations of known AHB and EHB colonies; delineate honeybee habitat parameters such as preferred vegetation community, climatic zone, elevation, and distance to water; investigate potential ecological consequences to native bees and other nectar-dependent species; monitor and detect habitat productivity changes; and develop computer models to illustrate and predict preferred AHB habitats and potential ecological consequences (Fig. 3).

The Future

Knowing how far north AHBs will spread is critical in predicting their ecological effects. There is general agreement that they have a climatic limit, but precise limits of their U.S. range expansion is disputed. Some researchers suggest that AHBs will disperse almost as far north as Canada; others propose that they will go no farther than the U.S. southwestern and southeastern corners. In all likelihood, AHBs will become established as a dominant ecosystem forager in the southern third of the United States, where EHB overwintering behavior is less critical for survival. If conditions are favorable, however, the AHBs may expand into marginally productive or colder habitats in higher latitudes or elevations.

While the ecological range limits and economic consequences of non-native AHB migration into the United States are not precisely known, researchers agree that honeybees are economically important, and that sufficient biological information exists to develop adequate inventory and monitoring programs. Added benefits to honeybee monitoring programs are also important because bee colonies can also serve as excellent indicators of flowering plant productivity, ecosystem stability, and relative ecological health.

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Bullfrogs: Introduced Predators in Southwestern Wetlands

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In the American Southwest, much of the native fish fauna is facing extinction (Minckley and Deacon 1991); frogs in California (Fellers and Drost 1993) and frogs and garter snakes in Arizona (Schwalbe and Rosen 1988) are also in critical decline. Habitat destruction and introduced predators appear to be primary causes of native frog declines (Jennings and Hayes 1994), and habitat modification often yields ponds and lakes especially suitable for introduced species. Introduced bullfrogs (*Rana catesbeiana*) have been blamed for amphibian declines in much of western North America (e.g., Hayes and Jennings 1986; Leonard et al. 1993; Vial and Saylor 1993). Extensive cannibalism by bullfrogs renders them especially potent predators at the population level. The tadpoles require only perennial water and grazeable plant material; hence, transforming young can sustain a dense adult bullfrog population even if alternate prey are depleted. This may increase the probability that native species may be extirpated by bullfrog predation.

Introduced predatory fishes are apparently an important cause of frog declines (Hayes and Jennings 1986). They have been strongly implicated in one important case of decline of native ranid frog (family Ranidae, the "true" frogs; Bradford 1989). Some introduced crayfish may also be devastating in some areas (Jennings and Hayes 1994). In our study region, however, neither introduced fishes nor crayfish are dominant. We present results that sustain a "bullfrog hypothesis" for some native ranid declines, and we present our study as an example of how evidence accumulates to support such a hypothesis.

In 1985 we began documenting historical localities for wetland herpetofaunas (reptiles and amphibians), based on museum records and personal interviews, then revisited these and additional areas to determine current species' status. Results of this process, plus circumstantial evidence, suggested that the bullfrog was a primary cause for declines of leopard frogs and garter snakes in southern Arizona (Schwalbe and Rosen 1988).

Courtesy J.N. Carr, Arizona Game and Fish Dept.

Fig. 1. The worm has turned! In this unstaged photograph taken at Parker Canyon Lake, Cochise County, Arizona, 1964, an introduced bullfrog is swallowing a Mexican garter snake, normally a frog-eating species. Such predation appears to be destroying remaining populations of this garter snake in the United States.

In 1986-89 and 1992-93 we conducted removal censuses of bullfrogs at San Bernardino National Wildlife Refuge (SBNWR), Cochise County, Arizona. We simultaneously monitored native Chiricahua leopard frogs (*R. chiricahuensis*) and Mexican garter snakes (*Thamnophis eques*) at the sites of bullfrog removal. A control site, with no bullfrog removal, was established in comparable habitat at Buenos Aires National Wildlife Refuge (BANWR), Pima County, Arizona.

Evidence for Bullfrog Effects

Bullfrogs ate garter snakes, including Mexican garter snakes (Fig. 1), as well as numerous frogs, including young bullfrogs and the last observed leopard frogs on our intensive study areas. In addition, these frogs ate other frogs and snakes, lizards, fish, birds, and mammals in addition to many invertebrates (*see* also Bury and Whelan 1984).

We currently know of no examples of overlap between populations of the native leopard frogs *R. chiricahuensis* and *R. yavapaiensis* and bullfrogs in southern Arizona. Leopard frogs were abundant at both SBNWR and BANWR before bullfrog proliferation, and as recently as 1981, bullfrogs and leopard frogs were both still widespread at SBNWR (D. Lanning, The Arizona Nature Conservancy, unpublished data). Leopard frogs apparently were extirpated from our SBNWR study area by 1989.

In 1993-94 relict populations of Chiricahua leopard frogs (2-20 adults each) were found 5, 10, and 19 km (3.1, 6.2, and 11.8 mi) east of SBNWR. These populations are in areas not occupied by bullfrogs in habitats that may dry too frequently for non-native predators (personal observations), as seen in native frogs of the central valley of California (Hayes and Jennings 1988). These recent findings near SBNWR further support the bullfrog hypothesis in southeastern Arizona.

Checkered garter snakes (*Thamnophis marcianus*) are semi-terrestrial and coexist in abundance with bullfrogs. The highly aquatic Mexican garter snake, however, has only small, apparently declining populations where its habitat overlaps with that of bullfrogs. Because the bullfrog is also highly aquatic, its effects on the Mexican garter snake have been greater than on the checkered.

Although Mexican garter snakes do reproduce where they occur with bullfrogs, few young survive (Fig. 2). Once the young snakes outgrow vulnerability to bullfrog predation, they survive well; young adults marked in 1986-88 have been recovered at ages 7-10 in 1993, equaling and exceeding known ages for garter snakes in the wild (Fitch 1965). All of the larger, older Mexican garter snakes have damaged tails from repeated bullfrog bites, and the largest and oldest one was found dying in 1993 with gross inflammation of the tail. It appears that without successful reproduction by some of these old snakes, the study population will shortly disappear.

Bullfrog Removal Experiments

Before 1993 intensive bullfrog removals were conducted two to three times per year at SBNWR. At one study pond, 854 large (80+ mm body length) bullfrogs had been removed from about 0.2 ha (0.5 acre) of habitat. After the 3 to 4 active-season months between removals, we saw a 50%-80% rebound toward preremoval numbers, and we observed weak evidence of positive effects on native leopard frogs and garter snakes (Schwalbe and Rosen 1988). Because a bullfrog can have as many as 20,000 eggs per clutch and has multiple clutches each year, the bullfrog was clearly uncontrollable at our initial level of effort.

Starting in 1993, we increased our efforts to remove bullfrogs from SBNWR by eliminating adult bullfrogs and catching juveniles as they matured.

Discussion

If adult-free bullfrog populations are attained at SBNWR during 1994, we predict that this will result in successful recruitment of juvenile Mexican garter snakes. We propose to translocate leopard frogs from nearby areas into fenced, newly created, bullfrog-free ponds. A primary objective is to have at least one natural area to save genetic stock of the local leopard frogs.

The SBNWR, with its numerous highly productive water sources, was probably a historical regional metapopulation (a set of populations connected by immigration and emigration) center (Gilpin and Hanski 1991) for leopard frogs. During times of drought, it was likely the mainstay of the species in the San Bernardino Valley system. Some of the unexplained frog declines in western North America (Cary 1993) may ultimately be traceable to catastrophic, localized extinctions in such refugia (Sjögren 1991; Bradford et al. 1993). An observation of probable rapid migratory spread by an introduced leopard frog species in Arizona (12 km/yr; Platz et al. 1990) suggests that individuals do disperse enough to consider metapopulation models. Information related to metapopulation phenomena could markedly enhance management for leopard frogs.

It is notable that the checkered garter snake, with an evolutionary background of geographical overlap with bullfrogs, succeeds with introduced bullfrogs in the West. Similarly, the accidentally introduced and rapidly spreading Rio Grande leopard frog (*Rana berlandieri*) in Arizona (Platz et al. 1990) also evolved with bullfrogs. In fact, this leopard frog is spreading into areas where the endemic Yavapai leopard frog (*R. yavapaiensis*) has been extirpated, probably by introduced predators as well as habitat alteration (Vitt and Ohmart 1978; Jennings and Hayes 1994).

Conclusion

Introduced predators such as the bullfrog can have devastating effects on faunas that evolved without equivalent predatory types. The bullfrog, as an exotic in the absence of key original enemies (the basses, pikes, snapping turtles, and water snakes of the eastern United States), attains tremendous population densities. Such non-native predators, in core population areas of native species, can lead to regional extinctions, and may account for some unexplained amphibian declines.

We now have abundant documentation that introduced predators, especially fish, crayfish, and bullfrogs, have caused major declines of frogs and other species in western North America. In Arizona, current trends suggest that inaction could lead to disappearance of three of five native leopard frog species within a decade. We urge, in addition to simply monitoring declines, active management where appropriate, within a controlled and documented framework. There is a pressing need for a practical, successful, and vigorously supported management strategy to preserve genetic stocks and restore habitats of native ranid frogs.

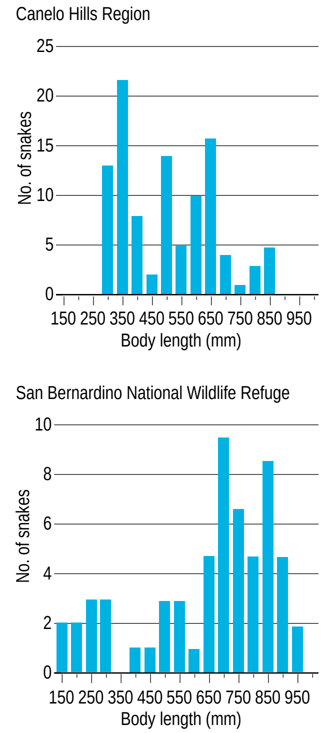

Fig. 2. Population structure of the Mexican garter snake. Numerous young snakes (200-700 mm, 1-3 years old) show successful reproduction in apparently intact populations (top), whereas bullfrog-affected populations (bottom) are composed mainly of older (700-1,000 mm, 3+ years old) snakes.

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Invasions of the Brown Tree Snake

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Brown tree snake (*Boiga irregularis*).

Courtesy G.H. Rodda

Around 1950, populations of the brown tree snake (*Boiga irregularis*) were introduced on Guam, a previously snake-free island. This introduction was the result of post-World War II traffic carrying military materials from the South Pacific region (Savidge 1987; Rodda et al. 1992). It resulted in major ecological changes and the loss of several bird and lizard species from the island starting in the 1970's and extending to the late 1980's. The severity of ecological damages resulting from this introduced snake may have been increased by the presence of other nonindigenous species, which served as alternative prey as native species declined.

The brown tree snake dispersed throughout Guam in the 1950's, 1960's, and 1970's, reaching high populations that resulted in devastating levels of predation on most native and introduced vertebrates (Savidge 1987; Engbring and Fritts 1988; Rodda et al. 1992). At the peak of the snake's irruption on Guam, densities probably exceeded 100 snakes/ha (40 snakes/acre), but following depletion of many of Guam's birds and mammals, snake densities appear to have fallen to 20-50 snakes/ha (8-20 snakes/acre; Rodda et al. 1992).

In the face of the loss of native forest birds and drastic reductions in other bird, mammal, and reptile species, the snake subsisted on smaller lizard prey and on introduced species, including lizards (*Hemidactylus frenatus* and *Carlia* cf. *fusca*), domestic poultry and cage birds, rodents (*Rattus* spp. and *Mus musculus*), house shrews (*Suncus murinus*), Eurasian tree sparrows (*Passer montanus*), and Javanese turtle doves (*Streptopelia bitorquata*). Thus, the reduction of snake densities that might have been expected after the loss of native prey species was limited because the snake could subsist on alternative introduced prey.

Species Lost from Guam

Since the arrival of the snake on Guam, the island has lost most of its indigenous forest vertebrates (Fig. 1). Too few baseline data are available to unequivocally determine the degree to which the snake is responsible for these losses, but several kinds of evidence create a strong case for the snake's role in the extirpation of many bird species (Savidge 1987, 1988; Conry 1988; Engbring and Fritts 1988) and several lizard species (Rodda et al. 1991). Additionally, some evidence exists that the snake played a role in the disappearance and decline of Guam's native mammals, three bat species (Wiles 1987), but no direct information is available for the two bat species that disappeared before 1980. The evidence clearly shows, however, that Guam has experienced a remarkably complete loss of its vertebrate fauna.

Even with all of the vertebrates at risk from the snake, the pattern of species' losses has followed a size gradient that is consistent with the snake's dietary habits (Engbring and Fritts 1988; Fritts 1988). Small birds, small mammals, and medium-sized lizards disappeared first and seem to have been most heavily affected. Contrary to what might have been expected, the most abundant bird species were affected first. We cannot determine if the abundance of the prey led to more effective search images for the snakes or if the ecological characteristics of the species and the habitats occupied contributed to this prey difference. The surviving native species and those that lasted the longest in the wild all exhibited extreme sizes (i.e., larger or smaller than those most affected) or some other trait that has minimized their vulnerability to snake predation.

Examples of these traits include large size: Mariana flying fox (*Pteropus mariannus*), Marianas crow (*Corvus kubaryi*), and Indian monitor lizard (*Varanus indicus*); urban dwelling: Micronesian starling (*Aplonis opaca*), mourning gecko (*Lepidodactylus lugubris*), and stump-toed gecko (*Gehyra mutilata*); cavity nesting: Micronesian starling and Micronesian kingfisher (*Halcyon cinnamomina*); cave ceiling roosting: gray swiftlet (*Aerodramus vanikorensis*); and extremely small size: mourning gecko and Marianas blue-tailed skink (*Emoia caeruleocauda*). All surviving endotherm populations (birds and mammals) consist of fewer than 1,000 individuals, and long-term population viabilities are in doubt for most of these groups on Guam.

Small lizards are much more numerous and have better long-term prospects even though evidence exists of localized extinctions caused by temporary surges in snake populations. The big tree gecko (*Gehyra oceanica*) has virtually disappeared since 1985, but its smaller congener (species in the same genus), the stump-toed gecko, persists in forested habitats in low numbers (Rodda et al. 1991). Some small introduced lizard species (mourning gecko, common house gecko, *Hemidactylus frenatus*, and brown four-fingered skink, *Carlia* cf. *fusca*) have expanded into new habitats in the absence of other species; they therefore maintain larger population levels on Guam even though they experience heavy predation by snakes.

The relative abundance of the Marianas blue-tailed skink has dropped markedly as the brown four-fingered skink increased after its arrival in Guam in the early 1950's (Fig. 2). Effects of predation by the snake and interactions between introduced lizards are evident in the relative abundances of lizard families, with the primarily arboreal gekkonids declining while the primarily terrestrial and more predation-resistant skinks have increased. Even introduced rodents and shrews show declines due to predation by snakes; trapping success for rodents and shrews was significantly reduced in 1984-85 compared to that of 1962-64 (Savidge 1987).

Risks of Dispersal from Guam

The many brown tree snakes on Guam make it probable that they may disperse as passive stowaways in ship and air traffic to other islands and the U.S. mainland (Fritts 1987, 1988; McCoid and Stinson 1991). To date, stowaway brown tree snakes have arrived in the northern Marianas Islands (Saipan, Rota, and Tinian); Marshall Islands (Kwajalein Atoll); Cocos Island near Guam; Okinawa; Diego Garcia in the Indian Ocean; Oahu Island, Hawaii; and Corpus Christi, Texas (Fritts 1988; unpublished manuscript). Verified and probable sightings of brown tree snakes span 1949-94 and show that dispersal of the brown tree snake is not uncommon. The apparent surge in the 1990's probably reflects better reporting of stowaway incidents rather than increased dispersal.

Risks of Damages from Further Colonizations

The islands adjacent to Guam are the northern Marianas, which have vertebrate faunas that are similar to Guam's, including some of the same introduced species. Like Guam, the northern Marianas have no native snakes. Thus, prey bases similar to those on Guam and capable of supporting high population levels of brown tree snakes exist in the northern Marianas, and species losses can be anticipated if the snake becomes established. For example, of 27 native resident bird species on the main islands of the northern Marianas (Saipan, Tinian, and Rota), 20 are shared with the original fauna of Guam and an additional 7 species are closely related to birds known from Guam. Guam and the northern Marianas also share five introduced bird species (Engbring et al. 1986). Six species of birds are federally listed as endangered or threatened in the northern Marianas, and all of these are conspecific (of or relating to the same species) or closely related to birds that have disappeared from Guam or declined significantly there (Engbring and Ramsey 1984; U.S. Department of the Interior 1990). Of 20 species of terrestrial amphibians and reptiles presently or formerly known from Guam and Cocos Island, 15 are shared with the northern Marianas, 8 native and 7 introduced (Rodda et al. 1991). Thus, the northern Marianas not only share the ecological vulnerabilities that led to mass extirpations on Guam, but also the bulk of the remaining habitat for Marianas' native species is on islands that have received stowaway snakes from Guam.

Hawaii suffered major losses in its vertebrate fauna after the arrival of the Polynesians and again after contact with Europeans. The state originally had 59 passerine bird species, but only 38 survived into historical times. Fifty species of passerines have been introduced in Hawaii, and those birds make up most of the land birds present today. At least 30 species of birds native to Hawaii are federally listed as threatened or endangered. One bird species native to Guam, the gray swiftlet, is established on Oahu (Moulton and Pimm 1986). Of the 14

Fig. 1. Status in 1993 of Guam's native forest vertebrates (those present in 1950) with estimates of the degree to which decline was due to the introduction of the brown tree snake.

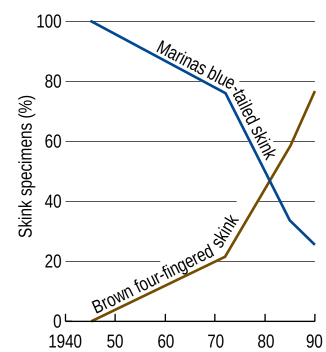

Fig. 2. Changes in the proportions of specimens of two common skinks in museum collections from Guam in four samples spanning 1945-90: Marianas blue-tailed skink (*Emoia caeruleocauda*) and brown four-fingered skink (*Carlia* cf. *fusca*).

reptile species present in Hawaii (all introduced), 8 are known as native or introduced species on Guam. Many of these introduced species are locally abundant and attain high population levels in Hawaii. All these factors show how capable the brown tree snake is in exploiting elements of the native and introduced fauna of Hawaii and in attaining high population levels in Hawaii and on other Pacific islands on which it may become established.

The effects of the brown tree snake extend beyond ecological damages; the snakes frequently climb on electrical transmission lines causing faults and disrupting electrical supplies, enter urban and residential areas where they consume poultry and pets, and bite humans causing trauma and serious health risks for small children (Fritts 1988).

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Wild Horses and Burros on Public Lands

by
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On December 15, 1971, Congress passed legislation to protect, manage, and control wild horses (*Equus caballus*) and burros (*E. asinus*) on public lands. The Wild Free-Roaming Horses and Burros Act (Public Law 92-195) described these animals as fast-disappearing symbols of the historic and pioneer spirit of the West. The Bureau of Land Management (BLM) and the U.S. Forest Service are charged with administering the law, which specifies how wild horses and burros are to be managed on the range and how excess animals are to be disposed. Section 3.(a) requires the Secretary of the Interior to manage wild free-roaming horses and burros in a manner designed to achieve and maintain a thriving natural ecological balance on public lands. This section also specifies requirements for inventorying, monitoring, establishing appropriate management levels, making removals, placing excess animals, and establishing criteria for destruction of animals.

Although these animals were once considered endangered by the nearly unrestrained onslaught of the mustangers and others, they have thrived under federal protection (Fig. 1). With few predators and with protection from humans, wild horse and burro populations on BLM-administered lands (where most of the animals are located) quickly grew until control of the populations and the effect on their habitat became a major concern.

Courtesy T. Pogacnik, BLM

Wild horses (*Equus caballus*).

The act requires that BLM maintain a current inventory of wild horses and burros on certain public lands. At present, BLM censuses each of the 196 herd-management areas on a rotating basis, usually every 3 years, using census techniques based on research published by the National Academy of Sciences (1982). Censuses in 1993 identified a nationwide population of 46,500 wild horses and burros (Fig. 2). Accuracy for the 1993 census ranged from 85% to 99% on wild horses and 75% to 88% on wild burros.

Annual population growth in wild horse herds varies from 5% to 25%, depending on range and environmental conditions, with 15% being a long-term average. At this rate of increase, wild horse populations may double in 5 years. The annual growth in wild burro populations has not been determined, but their reproductive capacity may be similar to that of wild horse herds.

The act specifies that wild horses and burros may be managed only on lands where they existed on December 15, 1971, the time of the act's passage. The population of wild horses and burros within those 1971 areas of use was estimated at 17,000 animals; however, at that time no formal inventory policies or procedures existed to census populations. The BLM now has 269 herd areas, 196 within which wild horses and burros are managed to some extent and 73 from which all wild horses and burros will be removed.

Wild horse and burro herd areas occupy almost 43 million acres (17.4 million ha) of public and private land in Arizona (about 4 million acres or 1.6 million ha), California (6 million+ acres or 2.4 million ha), Colorado (800,000+ acres or 324,000 ha), Idaho (450,000+ acres or 182,250 ha), Montana (55,000+ acres or about 22,275 ha), Nevada (nearly 19 million acres or nearly 8 million ha), New Mexico (nearly 150,000 acres or 60,750 ha), Oregon (nearly 4 million acres or 1.6 million ha), Utah (2.5 million acres or 1 million ha), and Wyoming (nearly 6 million acres or 2.4 million ha) (BLM 1993).

Within most herd areas, wild horses and burros graze with domestic livestock and a variety of indigenous wildlife species. Because they are generalist species, wild horses and burros inhabit a variety of habitats and vegetative communities.

The BLM's land-use planning process and evaluation of current inventory and monitoring data are used to determine a population level that maintains a thriving natural ecological balance with other uses. The act directs BLM to achieve appropriate population levels by removals, humane destruction, or other options, including antifertility methods.

BLM no longer destroys healthy excess wild horses and burros. Since 1973, when the first removals occurred, BLM has removed 141,762 wild horses and burros from public land and placed 122,627 animals into private care through the Adopt-A-Horse program.

Removing excess animals from populations that exceed appropriate numbers is expensive, has restricted BLM's attempts to pursue other management alternatives, and therefore has often allowed populations to increase dramatically. When populations reached crisis proportions, funding was increased and large numbers of excess animals were removed from the range and placed with private citizens through the adoption program. The number of animals removed often was greater than the number that could be adopted, resulting in high costs for feeding and veterinary services while animals were held pending adoption.

In June 1992 the Director of BLM approved the Strategic Plan for the Management of Wild Horses and Burros on Public Lands (BLM 1992). This plan represents BLM's first comprehensive policy for addressing wild horse and burro management. To reduce the frequency of removals, the plan recommends the use of antifertility management to slow population growth to a level where removals are only required on a cycle of 5 or more years instead of the current 3-year cycle. Pending the availability of practical and cost-effective fertility-control techniques, selective removal of animals based on age or sex is being used to reduce the growth rate in wild horse populations. The negative aspects of selective removal include the difficulty of predicting results through computer modeling and the extensive monitoring needed to ensure that age and sex ratios have not been altered to a level that could threaten the herd. Selective removals for controlling population growth are considered a temporary management option until research on immunocontraception is completed and can be implemented.

The BLM supports research on the use of immunocontraception for controlling wild horse population growth. Successful immunocontraceptive antigens have been developed; researchers are now trying to develop a system that would inhibit reproduction for 2 to 3 years (J.F. Kirkpatrick, Deacones Medical Research Institute, Billings, personal communication).

Before the passage of the act, wild horses and burros were often captured and destroyed as nuisances or were sold for profit, chiefly for use in commercial products. The methods employed in their capture and destruction were often less than humane. As public awareness of these animals grew, so too did support for federal legislation to protect them from inhumane treatment.

Public interest in the wild horse and burro program continues to direct implementation of the act. Since the act's passage in 1971, there have been 44 district court suits and in excess of 200 appeals of BLM decisions to the Interior Board of Land Appeals.

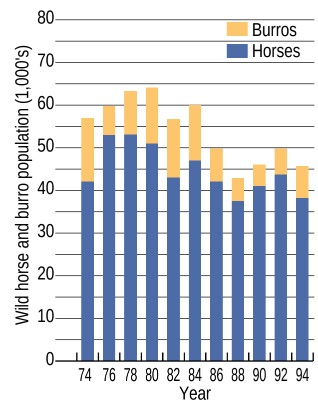

Fig. 1. Wild horse and burro population trends in BLM-administered lands since passage of the Wild Free-Roaming Horses and Burros Act of 1971.

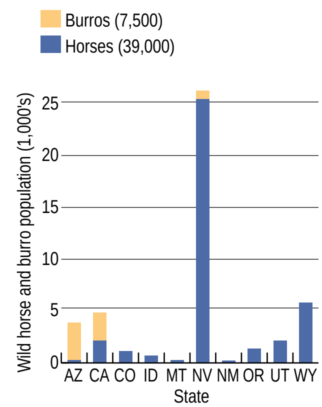

Fig. 2. Wild horses and burros in 1993: population by state.

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Purple Loosestrife

by
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Purple loosestrife (*Lythrum salicaria*) is an exotic wetland perennial introduced to North America from Europe in the early 19th century (Stuckey 1980). By the 1930's, the plant was well established along the New England seaboard. The construction of inland canals and waterways in the 1880's favored the expansion of purple loosestrife into interior New York and the St. Lawrence River Valley (Thompson et al. 1987). The continued expansion of loosestrife has coincided with increased development and use of road systems (Thompson et al. 1987), commercial distribution of the plant for horticultural purposes, and regional propagation of seed for bee forage (Pellet 1977). The plant now occurs in dense stands throughout the northeastern United States, southeastern Canada, the Midwest, and in scattered locations in the western United States and southwestern Canada. Newly created irrigation systems in many of the western states have supported its further spread.

Purple loosestrife is a classic example of an introduced species whose distribution and spread have been enhanced by the absence of natural enemies and the disturbance of natural systems, primarily by human activity. Although noted for the beauty of its late summer flowers, which also provide a nectar source for bees, loosestrife has few other redeeming qualities. Its invasion into a wetland system results in suppression of the native plant community and the eventual alteration of the wetland's structure and function (Thompson et al. 1987). Large, monotypic stands not only jeopardize various threatened and endangered plants and wildlife, such as Long's bulrush (*Scirpus longii*) in Massachusetts (Coddington and Field 1978), small spikerush (*Eleocharis parvula*) in New York (Rawinski 1982), and the bog turtle (*Clemmys muhlenbergii*) in the northeastern United States (Bury 1979), but they also eliminate natural foods and cover essential to many wildlife, including waterfowl (Rawinski and Malecki 1984).

Purple loosestrife has many traits that enabled it to become a nuisance in North America. A single, mature plant can produce more than 2.5 million seeds annually; these seeds are long-lived (Welling and Becker 1990) and easily dispersed by water and in mud, adhering to aquatic wildlife, livestock, and people (Thompson et al. 1987). Established plants are tall (about 2 m or 6.5 ft) with 30-50 stems forming wide-topped crowns that dominate the herbaceous canopy. A strong rootstock serves as a storage organ, providing resources for growth in spring and regrowth if the aboveground shoots are cut, burned, or killed by application of foliar herbicides. No native herbivores or pathogens in North America are known to suppress purple loosestrife (Hight 1990).

Courtesy R. Malecki, NBS

Purple loosestrife (*Lythrum salicaria*).

No effective method is available to control loosestrife, except in small localized stands that can be intensively managed. In such isolated areas, the plant can be eliminated by uprooting by hand and ensuring that all vegetative parts are removed. Other control techniques include water-level manipulation, mowing or cutting, burning, and herbicide application (Malecki and Rawinski 1985). Although these controls can eliminate small and young stands, they are costly, require continued long-term maintenance, and in the case of herbicides, are nonselective and environmentally degrading.

The most promising control measure for purple loosestrife is the application of classical biological weed-control procedures that use natural enemies like insects, mites, nematodes, and pathogens to reduce weed densities to tolerable levels. Results of insect surveys and screening tests conducted with the U.S. Department of Agriculture's Agriculture Research Service and the International Institute of Biological Control in Europe have identified five beetle species as potential control agents for purple loosestrife. Each species showed enough host specificity for purple loosestrife to be introduced with no ill effects to native North American plants.

Efforts are under way to rear large numbers of these insect species for further distribution and establishment in other states and provinces. A petition to introduce two of these beetles is under review by the USDA's Animal and Plant Health Inspection Service. Initial collection of these insects in Europe for release into the United States is planned for 1994.

A cooperative state and federal program for the biological control of purple loosestrife focuses on an international environmental weed problem that cannot be controlled by conventional means. With support from federal and state agencies we have brought together an

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international scientific advisory staff to participate in and oversee the selection, screening, and introduction of an insect predator community that will provide a long-lasting biological control mechanism for loosestrife, and which will also develop a corresponding program of research and evaluation.

Purple loosestrife is now a naturalized weed that always will be a part of most North American wetlands. Researchers hope that introducing select insects will result in replacing monotypic stands of loosestrife by native vegetation and an overall decrease in the occurrence of the plant. We predict a reduction of purple loosestrife abundance over the next 15-20 years to about 10% of its current level over about 90% of its North American range (Malecki et al. 1993).

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