

CHAPTER 5

Patterns, Modes and Extents of Invasions by Vertebrates

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5.1 INTRODUCTION

Within just the last 200 years human beings have transformed the globe, drastically altering its land, water, atmosphere, and life. Probably only in the few, poorly understood episodes of mass extinctions has the earth experienced such rates and magnitudes of change, and if present trends continue, the human impacts in the next century threaten to rival the natural catastrophes that occurred at the Permian–Triassic and Cretaceous–Tertiary boundaries (Nitecki, 1984).

Three interrelated activities of modern humans have drastically altered the distribution and abundance of living things and the structure and function of ecosystems on a truly global scale: (1) the transformation of the earth's surface into a landscape of fields, pastures, suburbs, cities, roads, reservoirs, canals, dumps, and mines; (2) the extraction and appropriation of the earth's physical and biotic resources to support the human population; and (3) the loss of biotic diversity owing to the disturbance of ecological communities, extinction of native species, and spread of exotics. Increasingly ecologists and biogeographers are being called upon to assess the rates and magnitudes of these changes, predict the future impact of human activities, and manage ecosystems so as to avoid or mitigate the most deleterious effects. The task of the present conference is to synthesize what is known about invasions of exotic species, and my job is to summarize information on 'patterns, extents and modes of invasions by vertebrates.'

This is a virtually impossible task for several reasons. First, this is not an area in which I can claim any special expertise beyond being a generalized community ecologist and biogeographer who has worked primarily with vertebrates. Second, the literature on vertebrate invasions is so vast that one would have to devote one's entire career in order to become a real expert on this subject. Third, the information that is available is widely scattered, of uneven quality, and of questionable comparability, making quantitative analyses difficult and suspect.

Given these limitations, I shall not attempt to synthesize all of the relevant data,

analyses, and interpretations. Instead, I offer a uniquely personal assessment of the state of our understanding of vertebrate invasions. First, I shall use examples from vertebrates to illustrate some of the general patterns and processes that characterize successful and unsuccessful invasions. These will be presented in the context of tentative rules that characterize attributes of species that influence their colonizing ability and attributes of environments that affect their susceptibility to invasion. Second, I shall show that these rules are of limited utility in making specific predictions about the probability of establishment of a particular species in a certain region or habitat. This unpredictability is due to the uniqueness of species and places, which in turn is in large part a consequence of their distinct histories. This influence of history complicates the interchange between basic ecologists, interested in general patterns and processes, and applied scientists, concerned with solving the case specific problems caused by alien species. Finally, I shall argue for a reassessment of scientific attitudes toward exotic species. The current trend toward homogenization of the earth's biota is inevitable. Given that anthropogenic habitat change and elimination of native species are likely to increase, the ability of certain species to tolerate human activities and invade disturbed habitats may provide one of the best hopes for preserving any functional ecosystems.

5.2 GENERAL PATTERNS AND PROCESSES

5.2.1 Patterns of successful invasion

There appear to be general patterns that can be induced from what is known about the differential success and failure of exotic vertebrates (Elton, 1958; Diamond and Case, 1986). Most of these inferences are necessarily qualitative, because the diverse data on different taxonomic groups, habitats, and geographic regions have not been assembled and analyzed quantitatively (but see Long, 1981). Nevertheless, I believe that these provisional generalizations could be developed much more rigorously, and I suspect that they apply equally well to plant and invertebrate groups that have been well studied, and probably to all organisms. I suggest that these might tentatively be called the rules of biological invasions. I develop five of these rules below, illustrate them with examples, and discuss some apparent exceptions.

Rule 1: isolated environments with a low diversity of native species tend to be differentially susceptible to invasion. The claim requires careful qualification. Those environments that are particularly susceptible to invasion by exotic species are generally those that are in some sense insular and have experienced low rates of natural colonization. They are usually characterized by small size, habitats that contrast markedly with the surrounding matrix, and a long history of effective isolation from similar environments that would be the most likely source of suitable colonists. Examples include oceanic islands such as Hawaii and

New Zealand, insular continents such as Australia and Madagascar, insular habitats such as lakes and desert springs, and other isolated distinctive environments such as the subtropical part of the Florida peninsula and the temperate tip of southern South America. When immigration rates have historically been low, increasing the rate of colonization (in this case through human transport) is likely to result in the establishment of new species. Qualified in this way, this rule is simply a restatement of one of the basic tenets of the theory of island biogeography (MacArthur and Wilson, 1967; Williamson, 1981) and the extension of the theory to other kinds of insular habitats (e.g., Brown and Gibson, 1983; Brown, 1986). Some environments have low biotic diversity because they are unproductive and/or physically harsh. They are not isolated by barriers from sources of potential colonists, and they are not particularly susceptible to invasion. Examples include the Sahara Desert and the tundra and taiga regions of northern North America and Eurasia.

Island biogeography theory predicts that, with equal opportunities for increased colonization, smaller and more isolated insular habitats should accumulate relatively larger numbers of alien species than larger and/or less isolated regions. In some circumstances the small, isolated islands will even be expected to acquire absolutely more species of exotics. This is largely a consequence of species-area relationships (e.g., see MacArthur and Wilson, 1967; Williamson, 1981; Brown and Gibson, 1983). Whenever similar environments are compared, large regions typically contain a larger sample of species than small ones. This holds for both insular habitats and nonisolated environments, but the species-area relationship for insular habitats characteristically has a steeper slope and lower intercept than for similar, but nonisolated environments (Figure 5.1). This is because insular habitats, surrounded by inhospitable environments, have high extinction rates; small islands cannot sustain species (such as many birds of prey and large mammalian carnivores and herbivores) that are constrained to occur at low population densities. Human activity usually reduces the effective isolation of insular habitats by increasing the rate of colonization by alien species. Although the quantitative increase in insular species richness will depend on the size of the pool of available colonists, whether or not native species go extinct, and other factors (see Schoener, 1974), given the range of species area relationships reported for habitats isolated to varying degrees, the result will sometimes be a greater increase in the absolute as well as the relative number of species in small, isolated habitats than in otherwise similar but larger and/or less isolated environments (Figure 5.1).

Figure 5.2 presents evidence that long-isolated regions with few species of native vertebrates are differentially susceptible to invasion. Because of their histories of exploitation by human colonists of British descent, Hawaii, New Zealand, Australia, and North America have had roughly comparable opportunities for colonization by exotics. For these four regions there is a strong negative relationship between percent of the fauna that is comprised of established exotics

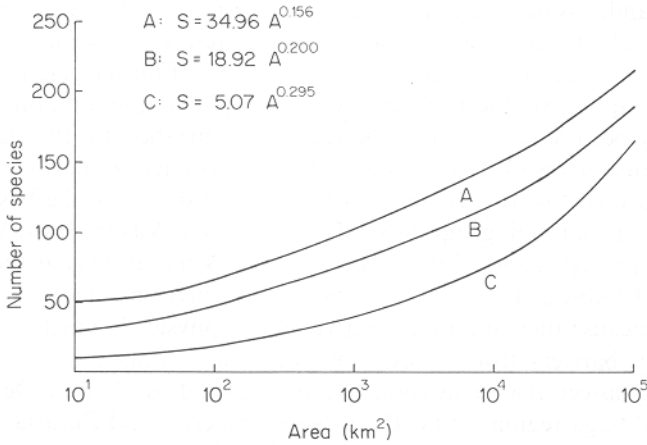


Figure 5.1. Hypothetical species–area relationships showing how previously isolated biotas should acquire additional species when colonization rates are increased as a result of human activity. The three curves show the expected equilibrium number of species (*sensu* MacArthur and Wilson, 1967) for areas with different degrees of isolation. The upper curve with a low slope and high intercept represents nonisolated sample areas of varying sizes within a large area, such as a continent. The lower curve with a steep slope and a low intercept represents historically isolated oceanic islands of varying sizes before invasion by aliens with human assistance. The intermediate curve represents the same islands after equal opportunity for invasion by alien species. Although species–area curves are usually plotted on logarithmic axes, here the ordinate is linear to show that small islands with few native species can sometimes be expected to acquire slightly more species than islands or continents with more diverse native biotas

and the number of native species. Interestingly, data points for birds and mammals seem to suggest approximately the same relationship. Percentages of exotics range from over 90% for mammals in New Zealand and Hawaii to less than 10% for both birds and mammals in Australia and North America.

Data for other vertebrate groups and other insular regions are consistent in suggesting that a large proportion of the species of isolated oceanic islands and other long-isolated environments is comprised of invaders. All of the nonmarine reptiles (14 species), amphibians (four species), and primary freshwater fishes (31 species) of the Hawaiian Islands have been introduced (McKeown, 1978; Maciolek, 1984). Fourteen (34%) of the 41 freshwater fish species of New Zealand are exotic (McDowall, 1978). Ten of 15 species of terrestrial mammals on the Galapagos are aliens (Thornton, 1971; H. Snell, personal communication). It is not only islands with depauperate biotas that are highly susceptible to invasion.

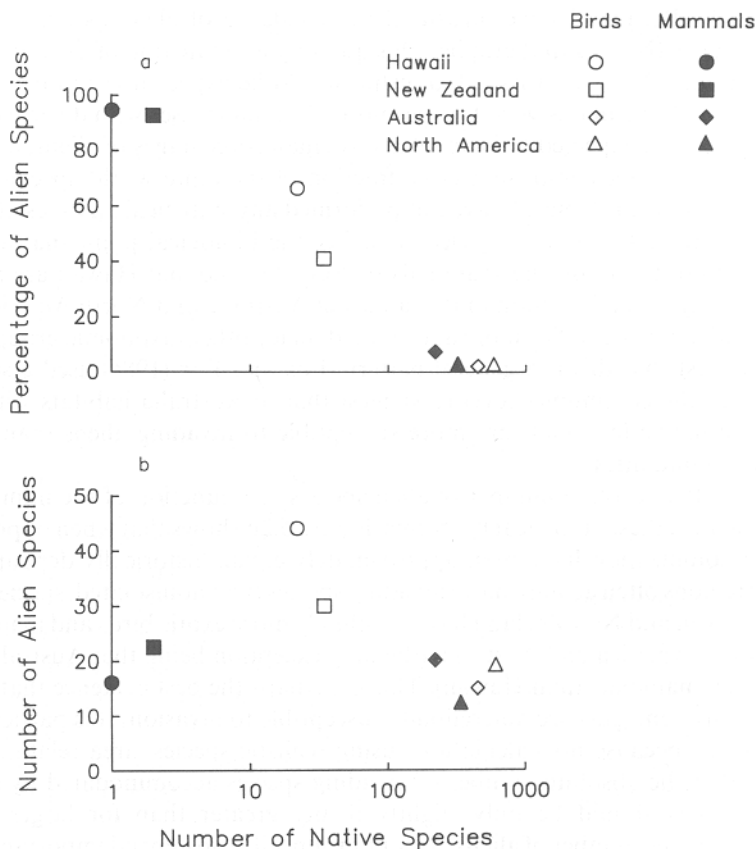


Figure 5.2. (a) The percentage of exotic species of mammals and birds in the total mammalian or avian fauna as a function of the number of native species for the Hawaiian Islands, New Zealand, Australia, and North America north of Mexico. (b) The absolute number of exotic species of mammals and birds as a function of the number of native species for these same four regions. Note that both ways of plotting the data suggest that historically isolated areas with low diversity of native species are differentially susceptible to invasion. Compiled from works cited in the text, de Vos *et al.* (1956), Falla *et al.* (1956), Kramer (1971), Pizzey (1980), van Riper and van Riper (1982), and other sources

Because of the low diversity and small area of aquatic habitats, the native fish fauna of the arid southwestern United States contains few species. The creation of artificial impoundments and introduction of exotics has greatly added to this number. For example, Minkley (1973) lists approximately 95 species that have bred in Arizona, and 67 (71%) of these have been introduced.

There are serious statistical problems with presenting data as I have in

Figure 5.2a. Because I have measured the incidence of alien species (A) as a percentage, $A/(N + A)$, and graphed this quantity as a function of the number of native species (N), a negative relationship would be expected even for random numbers analyzed in this way. Furthermore, the land masses with diverse native faunas would be expected to have relatively small percentages of aliens, because their native species comprise a large fraction of the finite world species pool. Because of these problems, I have not performed any statistical analyses of these data. Nevertheless Figure 5.2a clearly makes the biological point that a large proportion of the birds and mammals of New Zealand and Hawaii are aliens, whereas only a small fraction of the faunas of Australia and North America are comprised of invaders. The more anecdotal data for other taxonomic groups and areas suggest that this is a general pattern. Fox and Fox (1986) used a similar analysis at the community level to suggest that in Australia habitats with few species of native mammals are more susceptible to invading aliens than more diverse communities.

Plotting the absolute number of alien species as a function of the number of natives avoids these statistical problems. Figure 5.2b shows that when opportunities for colonization have been approximately equal, historically depauperate insular regions often acquire more invading species than nonisolated, species-rich areas. Hawaii and New Zealand have absolutely more exotic birds and mammals than North America and Australia (the only exception being that Australia has more alien mammals than Hawaii). This is perhaps the best evidence that these kinds of environments are differentially susceptible to invasion. It is particularly noteworthy, because my calculations using realistic species–area relationships suggest that the absolute number of invading species accommodated by small, isolated areas should be only slightly if any greater than for larger areas (Figure 5.1). The number of aliens at equilibrium will also depend importantly on the number of native species that have gone extinct; it is possible to accommodate more invaders if some of them ‘replace’ extinct natives. As mentioned below, isolated islands such as Hawaii and New Zealand have lost a substantial fraction of their endemic species, whereas larger land masses such as Australia and North America have suffered proportionately fewer extinctions.

Susceptibility of a region or habitat to invasion can also be assessed in terms of the impact of alien species on native biota and ecosystem function. There is abundant evidence that invading species not only comprise a large proportion of the biota in many small, isolated environments, they have also directly caused or indirectly contributed to the extinction of native species and substantially changed the structure and dynamics of both natural and human-modified ecosystems. The examples are overwhelming, even though only a few have been systematically quantified. The most important effects of exotic vertebrates can be attributed to predation (including herbivory) on native biota, competition with native species, effects of accompanying parasites and diseases, and disturbance of the physical environment. One of the best documented recurring effects is the

decimation of native sea and land birds by introduced rats and other predatory mammals on isolated oceanic islands (e.g., Atkinson, 1977, 1985; King, 1980, 1984). Table 5.1 summarizes some of the data compiled by King (1980) documenting the probable causes of extinctions of birds on islands throughout the world. Note that introduced predators are the single most important cause of extinctions, accounting for 42% of the total. Of those extinctions caused by predators, King attributes 54% to rats, 26% to cats, and the remainder to mongoose, weasels, stoats, and other species. Alien competitors and diseases account for an additional 7% and 6%, respectively, of the extinctions of island birds. Introduced mammalian herbivores, especially feral goats and pigs, have had equally dramatic but less thoroughly documented impact on the vegetation of small islands, causing extinctions of native species, pronounced changes in dominance and physiognomy, and indirectly affecting many other organisms (e.g. Holdgate and Nace, 1961; Coblenz, 1978; Diamond and Veitch, 1981; Loope and Scowcroft, 1985; Loope and Mueller-Dombois, this volume). The impact of exotic fishes as predators and competitors on native fishes and invertebrates in many small, isolated lakes and streams with depauperate native ichthyofaunas rivals that of alien mammalian predators on small oceanic islands. Introduction of fish, especially largemouth and smallmouth bass (*Micropterus salmoides* and *M. dolomieu*), mosquitofish (*Gambusia affinis*), and tilapia (*Tilapia mosambica*), has been accompanied by extinction of native species and pronounced changes in dominance and food webs in aquatic ecosystems as different as the Great Lakes of temperate North America (Smith, 1972; Moyle, 1986), small lakes in tropical Panama (Zaret and Paine, 1973), springs, streams, and lakes in the arid southwestern United States (Miller, 1972; Moyle, 1976), and streams in Hawaii (Maciolek, 1984).

Table 5.1. Apparent causes of extinction of birds on islands throughout the world since 1600 AD (from King, 1980; 1984). Note that predation, competition, disease, and genetic swamping, which together account for 57% of all extinctions, are all effects of alien species

	Indian Ocean	Atlantic Ocean	Pacific Ocean	Total
Predation	0	16	96	112
Competition	0	0	18	18
Disease	0	0	15	15
Genetic swamping	0	0	2	2
Hunting	7	13	20	40
Habitat destruction	1	5	46	52
Weather	0	1	0	1
Unknown	13	4	11	28
Total	21	39	208	258

It should be emphasized that impacts of alien species on native biota through indirect interactions can sometimes be as great or greater than the effects of direct competition or predation. Thus many effects of alien mammalian herbivores on the vertebrates and invertebrates of small oceanic islands are indirect. The direct effects of consumption of plants and disturbance of the physical environment cause major changes in vegetation and habitat (e.g. Holdgate and Nace, 1961; Coblenz, 1978; Diamond and Veitch, 1981). Alien species may also have indirect effects by facilitating the invasions of still more exotics. Of course this has been one of the most important effects of human colonization, but other vertebrates provide additional examples. A substantial part of the impact of introduced birds on the native avifauna of Hawaii is due to the alien populations importing and serving as a reservoir for avian malaria, an epizootic to which some native species are highly susceptible (van Riper *et al.*, 1986). Also in Hawaii, soil disturbance caused by the rooting of introduced pigs facilitates the invasion of native forest by exotic plant species (Smith, 1985).

There can be little doubt that the impacts of alien vertebrates in small, insular environments with depauperate native faunas are on average greater than their effects in larger, less isolated areas, such as continental habitats. Although the impact of exotics on continental biotas and ecosystems is sometimes substantial, I know of no case in which the extinction of a native species of terrestrial animal or plant on any of the major continental land masses can be attributed with reasonable certainty to the effect of an alien vertebrate (other than *Homo sapiens*). On the other hand, there are many well-documented cases of extinctions of insular animals and plants that can be attributed directly to predation by introduced mammalian carnivores or herbivores (see references above). Perhaps the most dramatic example is the extinction of the Stephens Island wren, whose demise can be reliably attributed to a single cat belonging to the lighthouse-keeper; in 1894 this animal 'collected' all 22 specimens known to science (King, 1984). But not all of these extinctions occurred long ago before the importance of conservation was widely recognized. King (1984) describes the case of Big South Cape Island, an important predator-free refuge in New Zealand until an irruption of rats in 1964 eliminated five species of birds and one of bats (one of the two land mammals native to New Zealand).

Rule 2: species that are successful invaders tend to be native to continents and to extensive, nonisolated habitats within continents. This rule is also a restatement of a long-held generalization of insular biogeography to the effect that there is a differential immigration from mainland to island. This is the basis of the so-called insular taxon cycle, which occurs if colonization is sufficiently infrequent that successful immigrants evolve into endemic insular species that are eventually replaced by new colonists (Wilson, 1961, MacArthur and Wilson, 1967; Ricklefs and Cox, 1972; Brown and Gibson, 1983). As an empirical generalization, this rule is illustrated in Tables 5.2–5.5. Of the introduced vertebrates of isolated oceanic islands, such as Hawaii (Table 5.2) and New Zealand (Table 5.3), the vast

Table 5.2. Identity and origin of the introduced land bird species of the Hawaiian Archipelago (from Long, 1981; Moulton and Pimm, 1986, 1987; and other sources). Unless specifically designated as being tropical, the native ranges of these species include temperate latitudes on the continent of origin. Although Hawaii is tropical, 17 of the 37 species (46%) are of temperate origin

Species	Native region
California quail (<i>Lophortyx californicus</i>)	North America
Chukar (<i>Alectoris chukar</i>)	Eurasia
Coturnix (<i>Coturnix coturnix</i>)	Eurasia
Jungle fowl (<i>Gallus gallus</i>)	Tropical Asia
Ring-necked pheasant (<i>Phasianus colchicus</i>)	Eurasia
Peafowl (<i>Pavo cristatus</i>)	Tropical Asia
Turkey (<i>Meleagris gallopavo</i>)	North America
Rock dove (<i>Columbia livia</i>)	Eurasia
Spotted dove (<i>Streptopelia chinensis</i>)	Asia
Zebra dove (<i>Geopelia striata</i>)	Tropical Asia
Skylark (<i>Alauda arvensis</i>)	Eurasia
Red-vented bulbul (<i>Pycnonotus cafer</i>)	Tropical Asia
Red-whiskered bulbul (<i>Pycnonotus jocosus</i>)	Tropical Asia
Melodious laughingthrush (<i>Garrulax canorus</i>)	Tropical Asia
Greater necklaced laughingthrush (<i>Garrulax pectoralis</i>)	Tropical Asia
Red-billed leiothrix (<i>Leiothrix lutea</i>)	Tropical Asia
Mockingbird (<i>Mimus polyglottus</i>)	North America
Shama (<i>Copsychus malabaricus</i>)	Tropical Asia
Bush warbler (<i>Cettia diphone</i>)	Asia
Hill myna (<i>Gracula religiosa</i>)	Tropical Asia
Common myna (<i>Acridotheres tristis</i>)	Tropical Asia
Japanese white-eye (<i>Zosterops japonica</i>)	Asia
Lavender waxbill (<i>Estrilda caerulescens</i>)	Tropical Africa
Orange-cheeked waxbill (<i>Estrilda melopoda</i>)	Tropical Africa
Red-cheeked cordon-bleu (<i>Ureaginus bengalus</i>)	Tropical Africa
Strawberry finch (<i>Amandava amandava</i>)	Tropical Asia
Common silverbill (<i>Lonchura malabarica</i>)	Tropical Asia
Spice finch (<i>Lonchura punctulata</i>)	Tropical Asia
Java sparrow (<i>Padda oryzivora</i>)	Tropical Asia
House sparrow (<i>Passer domesticus</i>)	Eurasia and North Africa
Western meadowlark (<i>Sturnella neglecta</i>)	North America
Cardinal (<i>cardinalis cardinalis</i>)	North America
Red-crested cardinal (<i>Paroaria cristata</i>)	South America
Yellow-faced grassquit (<i>Tiaris olivacea</i>)	Tropical America
House finch (<i>carpodacus mexicanus</i>)	North America
Yellow-fronted canary (<i>Serinus mosambicus</i>)	Tropical Africa
Saffron finch (<i>Sicalis flaveola</i>)	Tropical America

majority have come from diverse continental biotas, and the few other invaders have colonized from other islands with more speciose faunas. Vertebrates that have invaded continents, such as Australia (Table 5.4) and North America

Table 5.3. Identity and origin of the introduced mammals of New Zealand (from Gibb and Flux, 1973)

Species	Origin
Brush-tailed possum (<i>Trichosurus vulpecula</i>)	Australia
Red-necked wallaby (<i>Macropus rufogriseus</i>)	Australia
Hedgehog (<i>Erinaceus europeus</i>)	Eurasia
Rabbit (<i>Oryctolagus cuniculus</i>)	Eurasia
Hare (<i>Lepus capensis</i>)	Eurasia
Polynesian rat (<i>Rattus exulans</i>)	Southeast Asia
Black rat (<i>Rattus rattus</i>)	Eurasia
Brown rat (<i>Rattus norvegicus</i>)	Eurasia
House mouse (<i>Mus musculus</i>)	Eurasia
Weasel (<i>Mustela nivalis</i>)	Eurasia
Stoat (<i>Mustela erminea</i>)	Eurasia
Ferret (<i>Mustela furo</i>)	Eurasia
Cat (<i>Felis cattus</i>)	Eurasia
Pig (<i>Sus scrofa</i>)	Eurasia
Red deer (<i>Cervus elaphus</i>)	Eurasia and North America
Sambar (<i>Cervus unicolor</i>)	Tropical Asia
Japanese deer (<i>Cervus nippon</i>)	Asia
Rusa deer (<i>Cervus timorensis</i>)	Tropical Asia
Fallow deer (<i>Dama dama</i>)	Eurasia
Moose (<i>Alces americana</i>)	North America
Cow (<i>Bos taurus</i>)	Eurasia
Sheep (<i>Ovis aries</i>)	Eurasia
Goat (<i>Capra hircus</i>)	Eurasia
Himalayan thar (<i>Hemitragus jemlahicus</i>)	Asia
Chamois (<i>Rupicapra rupicapra</i>)	Eurasia

Table 5.4. Identity and origin of the introduced mammals of Australia (from Strahan, 1983; Myers, 1986)

Species	Origin
Rabbit (<i>Oryctolagus cuniculus</i>)	Eurasia
Hare (<i>Lepus capensis</i>)	Eurasia
Black rat (<i>Rattus rattus</i>)	Eurasia
Brown rat (<i>Rattus norvegicus</i>)	Eurasia
House mouse (<i>Mus musculus</i>)	Eurasia
Dingo (<i>Canis familiaris</i>)	Eurasia
Fox (<i>Vulpes vulpes</i>)	Eurasia
Cat (<i>Felis cattus</i>)	Eurasia
Horse (<i>Equus caballus</i>)	Eurasia
Donkey (<i>Equus asinus</i>)	Eurasia and North Africa
Pig (<i>Sus scrofa</i>)	Eurasia
One-humped camel (<i>Camelus dromedarius</i>)	Asia and North Africa

Table 5.4. (Contd.)

Species	Origin
Red deer (<i>Cervus elaphus</i>)	Eurasia and North America
Sambar (<i>Cervus unicolor</i>)	Tropical Asia
Rusa deer (<i>Cervus timorensis</i>)	Tropical Asia
Fallow deer (<i>Dama dama</i>)	Eurasia
Chital (<i>Axis axis</i>)	Tropical Asia
Hog deer (<i>Axis porcinus</i>)	Tropical Asia
Water buffalo (<i>Bubalus bubalus</i>)	Tropical Asia
Goat (<i>Capra hircus</i>)	Eurasia

Table 5.5. Identity and origin of introduced land bird species with established breeding populations in North America north of the United States–Mexican border (from Long, 1981; National Geographic Society, 1983; and other sources). Note that the vast majority of alien species in temperate North America originated in temperate regions of the Old World, whereas most of these exotics restricted to subtropical southern California and southern Florida invaded from tropical regions of the Old or New World

Species	Origin
<i>Temperate North America</i>	
Chukar (<i>Alectoris chukar</i>)	Eurasia
Black francolin (<i>Francolinus francolinus</i>)	Eurasia
Gray partridge (<i>Perdix perdix</i>)	Eurasia
Himalayan snowcock (<i>Tetraogallus himalayensis</i>)	Asia
Ring-necked pheasant (<i>Phasianus colchicus</i>)	Eurasia
Rock dove (<i>Columba livia</i>)	Eurasia
Ringed turtle-dove (<i>Streptopelia risoria</i>)	Eurasia
Monk parakeet (<i>Myiopsitta monachus</i>)	Temperate South America
Skylark (<i>Alauda arvensis</i>)	Eurasia
Crested myna (<i>Acridotheres cristitellus</i>)	Asia
Starling (<i>Sturnus vulgaris</i>)	Eurasia
Eurasian tree sparrow (<i>Passer montanus</i>)	Eurasia
House sparrow (<i>Passer domesticus</i>)	Eurasia and North Africa
<i>Restricted to subtropical southern California or southern Florida</i>	
Spotted dove (<i>Streptopelia chinensis</i>)	Asia
Rose-ringed parakeet (<i>Psittacula krameri</i>)	Tropical Asia and Africa
Budgerigar (<i>Melopsittacus undulatus</i>)	Australia
Canary-winged parakeet (<i>Brotogeris versicolorus</i>)	South America
Yellow-headed parrot (<i>Rhynchopsitta pachyrhyncha</i>)	Tropical America
Hill myna (<i>Gracula religiosa</i>)	Tropical Asia
Java sparrow (<i>Padda oryzivora</i>)	Tropical Asia

(Table 5.5) almost without exception have come from other continents, usually from larger ones with more diverse biotas.

This pattern, by itself, is not really sufficient to demonstrate differential invasive ability of species from diverse biotas, because opportunities for colonization may not be equal. Since continents and large habitats tend to have more species and larger populations than islands and restricted habitats, they would be expected to send out more colonists. Thus, even if the success rate of colonists were independent of their origin, we would expect asymmetrical exchange between diverse and depauperate biotas. Furthermore, because the dispersal of alien species is assisted by humans, patterns of commerce and peculiarities of culture affect the direction and probability of dispersal. Perhaps the most glaring examples were the naturalization or acclimatization societies formed by British colonists in North America, Australia, and New Zealand to promote the introduction of European songbirds and other plants and animals in order to provide familiar surroundings in foreign lands.

The fact that there are almost no good examples of successful invaders of continents that have come from small islands and other depauperate faunas (e.g. Tables 5.2–5.5), however, suggests that biotic resistance from diverse native species can be effective in repelling invaders. The susceptibility of southern Florida to many exotic vertebrates, including some from islands in the Caribbean, is an apparent exception, but actually one that supports the rule. Southern Florida is an ecological island of tropical, subtropical, and human-modified habitats, with a highly depauperate and endemic vertebrate fauna. It has proven susceptible to invasion by many alien vertebrates, including 25 species of reptiles and amphibians. Among the latter, six species from the diverse *Anolis* lizard fauna of the Greater Antilles have successfully colonized the small island of mesic tropical habitat provided by suburban Miami, Florida (Wilson and Porras, 1983).

Although it seems logical that the larger the biota, the higher the probability that it will contain competitors or predators capable of inhibiting initial population growth of a new colonist sufficiently to prevent its establishment, it is hard to test this conjecture. Both competition and predation can potentially be concentrated in a few, strongly interacting, specialized species or diffused among many, generalized species. Since abiotic factors and chance events can also affect the fate of invaders, it is usually very difficult to identify the cause(s) for the success or failure of a particular colonization.

These problems can potentially be overcome by statistical analysis of large samples of exotic species and the biotas they have or have not been able to invade. Moulton and Pimm (1986, 1987) have been able to compare attributes of the many successfully and unsuccessfully introduced land bird species in the Hawaiian Archipelago, and their analyses suggest that competition from native and previously established exotic species has played a significant role. Success of exotics was higher on islands and in habitats where the diversity of established

species was lower, and successful invaders tended to be more different in morphology from (and hence presumably less likely to compete with) resident species than unsuccessful introduced species. Fox and Fox (1986) reach similar conclusions about the ability of alien mammals to invade local communities in Australia.

It might be expected that absence or low diversity of predators would also facilitate establishment of exotics. I know of no direct data to support this prediction. However, the devastating effects of introduced predators and pathogens on the native vertebrates of many oceanic islands suggests that native enemies are either absent or much less effective than the predators from diverse continental biotas. Although this is somewhat indirect evidence, it strongly suggests that colonists of depauperate islands and habitats should usually face less severe predation than they experienced in the diverse biotas where they originated.

Rule 3: successful invasion is enhanced by similarity in the physical environment between the source and target areas. This pattern probably can be attributed primarily to the direct effects of physical factors in limiting the abundance and distribution of populations of vertebrates. In addition, however, availability of food resources and attributes of coexisting species tend to be correlated with physical variables. Consequently, colonists are more likely to be able to invade environments that provide climatic, geological, limnological, and oceanographic conditions similar to where they originated.

This rule is difficult to quantify accurately without analysis of the entire geographic ranges of species and of physical conditions in both source and target regions. Tables 5.2–5.5 provide much less precise information. Nevertheless it is apparent that the temperate regions of North America and Australia have been colonized almost exclusively by species that are native to temperate regions of Europe, Asia, and North Africa. Similarly, exotics from tropical America and Southeast Asia have been relatively successful in colonizing the small subtropical to tropical regions of southern Florida, southern California, and northern Australia. There are some conspicuous exceptions to this rule. In Australia, for example, species of temperate-zone origin, such as brown rat (*Rattus norvegicus*), house mouse (*Mus musculus*), and donkey (*Equus asinus*) have invaded tropical habitats, whereas the tropical rusa deer (*Cervus timorensis*) and hog deer (*Axis porcinus*) have become established in temperate regions. The reason for this lack of precise correspondence between the physical environments of source and target areas seems fairly straightforward. Many vertebrates can tolerate a much wider range of physical conditions than they encounter within their native geographic and habitat ranges. As long as these broad tolerances are not exceeded, they may invade whenever the biotic environment offers an abundance of food and a relative absence of competitors and predators. For example, largemouth bass (*Micropterus salmoides*) from temperate North America has been successfully introduced into tropical and subtropical lakes and reservoirs

around the world (e.g. in central Africa, Central America, the West Indies, and Hawaii).

Islands and other depauperate regions provide many exceptions to this rule. Thus, although the Hawaiian Islands are tropical, a relatively large proportion of the mammalian, avian, and amphibian exotics have come from temperate regions (Table 5.2). Similarly, of the 67 species of exotic freshwater fishes in Arizona reported by Minkley (1973) at least 21 have native ranges confined to more northerly latitudes in North America or Eurasia, and at least 10 species are native to more tropical regions of the Americas or Africa. The fact that similarity of physical environments of source and target seems to have less effect on success of invaders when the diversity of the target biota is low suggests the interesting possibility that exotics can tolerate a greater variety of abiotic conditions when the biotic resistance is low.

Rule 4: invading exotics tend to be more successful when native species do not occupy similar niches. This rule is related to Rules 1 and 2, above, and like them suggests that competition from native species with similar requirements plays a significant role in resisting invaders. Space does not permit a discussion of how to measure niches and whether unfilled niches exist. Suffice to say that many successful invaders exhibit tolerances for abiotic and biotic conditions and use habitats and resources differently from native species. Good examples are provided by the birds and mammals that have successfully colonized relatively undisturbed habitats in either North America or Eurasia from the other landmass. North America has no native ecological equivalents of the horse, donkey, or chukar partridge (although horses inhabited North America in the Pleistocene), and Europe has no truly amphibious rodents equivalent to the muskrat and coypu (which is native to South America, although it has also invaded the southeastern United States). Perhaps the best continental example is provided by comparison of the Australian bird and mammal faunas. Because of the superior ability of birds to colonize across water barriers, the native Australian avifauna is diverse and contains representatives of many orders and families; in contrast, native mammals consist only of monotremes, marsupials, rodents, and bats. The number of established introduced bird and mammal species is about the same (approximately 20). But, only two birds, the European blackbird (*Turdus merula*) and the mallard duck (*Anas platyrhynchos*) have spread into relatively undisturbed habitats (Fox and Adamson, 1980). This is in dramatic contrast to the mammals; at least 12 species (two lagomorphs, three carnivores, and at least seven ungulates) that have no ecological vicars in the native fauna have spread widely to colonize undisturbed habitats (Fox and Adamson, 1980; Strahan, 1983; Fox and Fox, 1986; Myers, 1986).

The same pattern is seen on oceanic islands. Because of their differential abilities to colonize over saltwater barriers, native terrestrial mammals and freshwater fishes are few or absent on isolated islands whereas land birds are much better represented. Introduced fish and mammals have in general been

more successful than birds in colonizing such islands and especially in becoming established in undisturbed habitats.

Rule 5: species that inhabit disturbed environments and those with a history of close association with humans tend to be successful in invading man-modified habitats. This is really an important special case of Rule 4, above. There are many examples (see also Orians, 1986). Establishment of exotic fishes in the southwestern United States has been enormously facilitated by construction of reservoirs in a region where natural lakes were almost nonexistent. More than half of the 67 species of exotic fishes in Arizona are confined to artificial impoundments. More species of Eurasian vertebrates have become established in North America than vice versa. Most of the successful Old World invaders are very successful around human habitation in their native region, and they are largely restricted to urban, suburban, and agricultural ecosystems in the New World (e.g. black rat (*Rattus rattus*), brown rat, house mouse, house sparrow (*Passer domesticus*), starling (*Sturnus vulgaris*), rock dove (*Columbia livia*), ring-necked pheasant (*Phasianus colchicus*), and gray partridge (*Perdix perdix*)). If these species are discounted, then the number of exotics that have been able to colonize relatively undisturbed habitats on either landmass is small and much more symmetrically distributed with respect to continent of origin (e.g. Old World brown trout (*Salmo trutta*), horse (*Equus caballus*), donkey, and chukar partridge (*Alectoris chukar*) in North America, and North American largemouth bass, gray squirrel (*Sciurus carolinensis*), muskrat (*Ondatra zibethica*), and mink (*Mustela vison*) in Eurasia). Even on remote oceanic islands, many of the exotic vertebrates are associated with humans in their native regions and their successful colonization must be attributed in part to their ability to exploit disturbed habitats.

To some extent this may reflect the bias that commensal species are more likely to be accidentally or intentionally introduced. However, it is still the case that these exotics tend to thrive in disturbed environments and to be much less successful in invading relatively pristine habitats. For example, in both the Hawaiian Islands (Moulton and Pimm, 1986) and New Zealand (personal observation), exotic bird species have been very successful in invading urban, suburban, and agricultural habitats and much less successful in establishing themselves in native forest. In contrast, many native species persist in relatively undisturbed habitats, but most of these natives have not been able to survive in habitats that have been substantially modified by human activities.

5.2.2 Modes and extents of invasion

The modes of colonization of most of these exotic vertebrates are known. The vast majority have been introduced, either deliberately or accidentally, by humans. The first introductions occurred as a result of the colonization and subsequent movements of primitive man. Fossil records from isolated oceanic

islands are beginning to provide information on the surprisingly large impact of early humans on the biota (e.g., Olson and James, 1982; Morgan and Woods, 1986). Early human colonists not only caused the extinctions of many native species, they also brought with them the first exotics. Among the well-documented introductions of vertebrates by primitive humans are the dingo (*Canis familiaris dingo*) in Australia, the Polynesian rat (*Rattus exulans*) on many Pacific islands, and at least seven species of lizards on Hawaii (Oliver and Shaw, 1953). Of course the 'discovery' of the rest of the world by Europeans and the subsequent development of worldwide travel and commerce led to the great wave of introductions that has occurred within the last few centuries. Vertebrates were transported to foreign islands and continents accidentally in ships, planes, and their cargos. For example, the commensal rats (*Rattus rattus* and *R. norvegicus*) and the well-named house mouse (*Mus musculus*) and house sparrow (*Passer domesticus*) accompanied Europeans as they colonized the world. Many vertebrates were deliberately introduced for a wide variety of reasons: food (e.g. rabbit (*Oryctolagus cuniculus*) in Australia, goat (*Capra hircus*) on Aldabra, and pig (*Sus scrofa*) on Hawaii), sport (e.g. red deer (*Cervus elaphus*) in New Zealand, chukar partridge in North America, and rainbow trout (*Salmo gairdneri*) in Chile and New Zealand), biological control of pests (e.g. fox (*Vulpes vulpes*) to control rabbits, and giant toad (*Bufo marinus*) to control cane beetles in Australia, mongoose (*Herpestes auropunctatus*) to control rats in the Hawaiian and Antillean Archipelagos), and aesthetics (e.g. songbirds in Hawaii, house sparrow and starling in North America, and grey squirrel in Europe). Still other species were imported originally as domestic animals, furbearers, or pets, but subsequently escaped from captivity (e.g. camel, donkey, horse, and goat in Australia, several species of tropical fish and parrots in southern Florida, mink and muskrat in Europe, and horse and donkey in western North America).

It is surprising, given the disastrous impacts of some introduced species, that exotic vertebrates continue to be imported at amazingly high rates. Government agencies are gradually becoming more cautious, but they continue to introduce deliberately species for fishing, hunting, and biological control. The pet trade, perhaps the single largest source of current introductions, continues to import large numbers of exotic species with only minimal regulation in most countries.

There is such a wide range of dispersal modes, that it becomes difficult and arbitrary to define an invading or exotic species. For example, in addition to those species that have been transported across major biogeographic barriers and introduced into new areas, there are many species whose dispersal has clearly been facilitated by human activities, but which have travelled under their own power to invade new regions. Some of these have taken advantage of man-made corridors to cross previously impenetrable barriers. For example, the predaceous sea lamprey (*Petromyzon marinus*) was able to invade the upper Great Lakes, where it decimated native populations of lake trout (*Salvelinus namaycush*) and whitefish (*Coregonus* spp.), after construction of the Welland Canal enabled it to

bypass Niagara Falls (Smith, 1972; Moyle, 1986). Similarly, the Suez Canal has enabled at least 30 species of fish to colonize the eastern Mediterranean Sea from the Red Sea (Por, 1971; 1977). Changes in habitat and the availability of resources have permitted many native species to expand their ranges and invade new regions. For example, when the forests of northeastern North America were cleared for agriculture in the last century, several birds and mammals from prairie habitats shifted their ranges hundreds of kilometers eastward. These include the meadowlark (*Sturnella magna*), bobolink (*Dolichonyx oryzophorus*), coyote (*Canis latrans*), and prairie deer mouse (*Peromyscus maniculatus bairdii*). Similarly, within the last century in both Europe and eastern North America several songbird species have extended their ranges far to the north in apparent response to man-modified habitats, increased food availability, and perhaps climatic change. Clearing of forest and introduction of domestic livestock appears to have enabled the cattle egret (*Bubulcus ibis*) to colonize South America from Africa (and then subsequently to invade North America) and Australia from southern Asia.

The extents of invasions are enormously variable. Some species, such as the commensal black and brown rat, and house mouse, have become almost cosmopolitan as they have followed Europeans to all corners of the globe. But by no means all widespread invaders are commensal or even associated with human disturbance. The rabbit, fox, dingo, and feral cat inhabit virtually the entire Australian continent, including many virtually pristine habitats. In the 80 years since its accidental release in Czechoslovakia, the muskrat has expanded to occupy as large a geographic range in Eurasia as in its native North America. In contrast, other species, such as chital and hog deer in Australia and the crested myna and skylark in North America, have become firmly established, but only within a very local region, and they do not appear to be spreading. Even among closely related, ecologically similar species the contrasts are striking. For example, in a little over a century since its introduction into the northeastern United States, the house sparrow has spread to occupy virtually the entire North American continent and to become one of the most abundant bird species (Robbins, 1973). On the other hand, its congener, the European tree sparrow (*Passer montanus*), remains confined to a few thousand square kilometers in the central United States, where it is well established but not abundant.

How do we account for this enormous variability? To what extent are founder events, genetic adaptations, life history traits, population dynamics, interactions with other species, and relationships with the physical environment responsible for the extents of invasion by different exotic species? At present these questions have been addressed for a few vertebrate species. Studies of the giant toad and rabbit (e.g. Myers, 1971; Cooke, 1977; van Beurden, 1981) in Australia were motivated by the practical importance of assessing the probable geographic spread, ecological and economic impacts, and means of biological control for these pests. These efforts were successful in understanding the factors that

contributed to the success of these species, in predicting their eventual limits of distribution, and, at least in the case of the rabbit, in attaining a certain measure of control. Studies of the house sparrow in North America (e.g. Johnston and Sealander, 1973; Johnston and Klitz, 1977) and the house mouse in Europe and North America (e.g. Berry, 1978; 1986) have elucidated some of the genetic and evolutionary processes that have accompanied colonization. It should be noted that all of these studies were *ad hoc*, made after the exotics were already enormously successful. They are valuable, but they provide few gratifying generalizations about the factors that are responsible for initial establishment, limit the extent of invasions, and account for the great variation in success among species.

5.3 CAN INVASION BIOLOGY BE MADE A PREDICTIVE SCIENCE?

5.3.1 A thought experiment with Andean sparrows

The general rules developed above suggest that at one level, it is possible to characterize attributes of successful and unsuccessful invasions and thus to make certain kinds of qualitative predictions. For example, the Andean sparrow (*Zonotrichia capensis*), a native finch widespread in both relatively pristine and highly disturbed habitats in Central and South America, is more likely to be successfully introduced into New Zealand, where land bird diversity is low, than into a climatically similar region of eastern North America or Europe, where avian diversity is much higher. Further, this temperate and high-elevation tropical species would be more likely to become established on temperate Easter Island than on low, tropical Christmas Island. Also, it would be more likely to colonize eastern Europe, where there are few ecological equivalents of sparrows, than western North America, where there are several closely related, ecologically similar species. If the Andean sparrow became established in New Zealand, it should be more successful around human habitations than in undisturbed native forest. Finally, in all of these situations the Andean sparrow would be more likely to be a successful invader than the closely related golden-crowned sparrow (*Zonotrichia atricapilla*), which appears to have narrower requirements, occurs at lower densities in restricted habitats in western North America, and is seldom found in highly human-modified environments.

But all of the above are very general, qualitative predictions. It is another matter entirely to replace the 'more likely' in any of the above statements with an accurate quantitative estimate of the probability of success. The patterns and processes discussed in the previous section may provide the basis for predicting the relative susceptibility of different regions to invasion and the relative chances of success of different kinds of exotic species, but they provide little basis for predicting the probability of success of any particular species at any given site.

What would be required to make such a specific prediction—for example, to predict whether the Andean sparrow would become established on the South Island of New Zealand? The success of this introduction should depend on: the number of birds introduced; their sex ratio, age structure, health, parasite load, and genetic constitution; the time of year of their introduction; the geology, climate, vegetation, availability of appropriate foods, and the kinds of competitors, predators, and pathogens both at their place of origin and at the release site; and many other variables (see also Ehrlich, 1986). In short, what is required is a thorough, species-specific study of the population biology and niche of the Andean sparrow, and an equally careful assessment of the biotic and physical environment at the release site. Even more information would be desirable. If establishment were likely, it would be important to know over what area and into what habitats the new exotic would spread, what population densities it would attain, and what impact it would have on native species and on humans. This is a tall order. It requires more information than is presently available for any vertebrate species.

5.3.2 History, uniqueness, and predictability

This thought experiment demonstrates the difficulty of making invasion biology a precise, predictive science. It exposes the limitations of our ecological and evolutionary knowledge, and the difficulties of applying our limited knowledge to practical problems. Most of the problems caused by exotics are species-specific, but by definition each species is unique. It has a unique history and a unique ecological niche—a special combination of tolerances, requirements, and relationships with other organisms—that reflects the constraints of its ancestry and the influences of its past environments. This historically based uniqueness characterizes all levels of biological organization, from cells and individuals, through communities and species, to the entire biosphere. Furthermore, the environments, as well as the organisms, are unique. Each continent, ocean, island, lake, stream, and local patch of habitat has a special combination of physical conditions and biotic composition that also reflects its unique history. This kind of uniqueness renders certain kinds of prediction impossible, or at least impractical. When each unit has its own special attributes, it is impossible to predict the behavior of an individual unit without knowing all of these attributes and their dynamical consequences.

Because of this historically based uniqueness of both exotic species and their environments, the study of biological invasions has been and will continue to be the study of both general trends and special cases. The trends hold because there are systematic differences among the units. For example, islands are smaller in size, isolated by barriers to dispersal, and have a narrower range of physical conditions and fewer species than continents; geographically widespread species interact with a wider variety of physical conditions and more other species than

narrowly endemic forms. But the behavior of the individual units is always somewhat unpredictable, because there are important differences even between islands in the same archipelago or species in the same genus.

5.3.3 Applications to specific problems

Basic ecologists, evolutionary biologists, and biogeographers, in search of general trends and mechanisms, will often be content to sacrifice precision for generality. They will continue to use invading species as invaluable experiments to help them understand the structure and dynamics of communities and biotas. Applied biologists, with specific problems to solve, cannot be satisfied with imprecise generalities. They will continue to deal with invading species largely on a case-by-case basis. Just as when dealing with similar problems, such as biological control of pests and preservation of rare and endangered species, they will have to take account of the unique, historically based attributes of each species and environment.

There are two lessons in this. First, just as the goals of basic and applied scientists differ, so does the kind of science that is necessary to pursue these goals. This is no grounds for lack of dialogue and cooperation between basic and applied ecologists. However, in order for such interaction to be productive, each must recognize the reality of this spectrum between general trends and unique attributes, and try to bridge the gap. This spectrum is a phenomenon of natural systems, not a creation of obstinate scientists. Second, there are limits to what both basic and applied biologists can contribute to solving practical problems. That particular problems caused by an exotic species in a certain area must always be dealt with on a case-by-case basis does not necessarily reflect on the inadequacy of basic ecological knowledge or the failure to apply general concepts to specific situations. Instead it is a necessity imposed by the historically based uniqueness of both organisms and their environments. Because of the complexity and uniqueness of these systems, the knowledge necessary to manage them precisely is vast. The public and the politicians must be understanding, patient, and willing to pay the costs.

It is in part because of the uniqueness of species and places that there is little pattern in the management of exotic vertebrates. Perceived costs and benefits of exotics and strategies for their elimination or management vary on a case-by-case basis. Some countries, such as Australia and New Zealand, devote massive efforts to strict quarantines to keep out new invaders and to control or eliminate many species that have previously invaded. Other countries, including the United States, continue to import game fishes, birds, and mammals, transplant them to new localities, and manage them for increased populations. The success of management schemes has also been enormously variable; some alien vertebrates have been eliminated, whereas others remain abundant pests despite long-standing, costly efforts to control them. Although there are many well-studied case histories, I doubt that it is useful to make generalizations.

5.4 THE PLACE OF EXOTICS IN A DISTURBED BIOSPHERE

Unless one is a fisherman, hunter, or member of an acclimatization society, there is a tendency to view all exotic vertebrates as 'bad' and all native species as 'good.' For example, most birdwatchers, conservationists, and biologists in North America view house sparrows and starlings with disfavor, if not with outright loathing; they would like to see these alien birds eliminated from the continent if only this were practical. There is a kind of irrational xenophobia about invading animals and plants that resembles the inherent fear and intolerance of foreign races, cultures, and religions. I detect some of this attitude at this conference. Perhaps it is understandable, given the damage caused by some alien species and the often frustrating efforts to eliminate or control them.

This xenophobia needs to be replaced by a rational, scientifically justifiable view of the ecological roles of exotic species. In a world increasingly beset with destruction of its natural habitats and extinction of its native species, there is a place for the exotic. Two points are particularly relevant. First, increasing homogenization of the earth's biota is inevitable, given current trends in the human population and land use. Despite efforts to prevent them, biological invasions will continue, and some proportion of them will be successful. Deliberate and accidental introductions will continue to supply many of the immigrants, but species will also invade under their own power, moving into favorable habitats that have been altered by human activities. Geographically restricted native species with sensitive requirements will continue to have high extinction rates, and those widespread, broadly tolerant forms that can live with humans and benefit from their activities will spread and become increasingly dominant.

The second point is that exotic species will sometimes be among the few organisms capable of inhabiting the drastically disturbed landscapes that are increasingly covering the earth's surface. As humans devote an increasing share of the earth's physical resources and biological productivity to supporting their own population, and do so with low efficiency, the share of resources and productivity that remains to support wildlife must diminish (Vitousek *et al.*, 1986). Urban, suburban, and agricultural areas are ecosystems. They and the less modified grazing and timber lands are managed to support human populations and certain animal and plant species that directly benefit humans. If these ecosystems are managed appropriately, they can also support wildlife, including a surprising variety of vertebrates. Sometimes these can be native species, but sometimes the choice may be between exotics or virtually no wildlife at all. Because of their large body sizes, high energy requirements, and low population densities, vertebrates in general are susceptible to local and total extinction; endemic species with narrow requirements and restricted distributions are especially sensitive. Fortunately, other vertebrates can withstand and even benefit from human activities; unfortunately many of these are alien species and many others are natives that are widely distributed, common, and often viewed as 'pests.' The term pest seems to

include any species that manages to obtain a significant share of the productivity of ecosystems that are managed for anthropocentric goals; pests consume agricultural products destined for human consumption, suppress domestic plant and animal populations through competition or predation, and compete with or prey upon aesthetically desirable native species.

The role that aliens may play is illustrated by the introduced vertebrates in the grounds of the East-West Center where this conference was held on the outskirts of Honolulu in the Hawaiian Islands. The park-like surroundings were beautifully landscaped with trees, flowers, and a cascading stream. I identified more than ten birds, a lizard, a frog, and several species of fishes, all introduced. On the one hand this might be considered a depressing example of just how 'disturbed' the lowlands of Oahu have become. On the other hand, it could be considered an encouraging example of the kind of diverse and aesthetically appealing vertebrate biota such a human-modified environment can support. One thing is certain: if all of the alien vertebrates were eliminated, few if any native species would take their places. If this provides a glimpse of what the future holds for many areas throughout the world, it is not an altogether pessimistic view.

This is not to say that we should halt our efforts to conserve undisturbed habitats and native species, including safeguards to prevent the invasion of harmful exotics. In most cases native species should be preferred over aliens, because natives will be less likely to have unanticipated disastrous effects, either within highly managed ecosystems or in less disturbed adjacent habitats. But I also suspect that increasingly even the 'natives' will be invaders, in the sense that they will be broadly tolerant, common species that have expanded their habitat and geographic ranges to exploit highly disturbed environments.

It has become imperative that ecologists, evolutionary biologists, and biogeographers recognize the inevitable consequences of human population growth and its environmental impact, and that we use our expertise as scientists not for a futile effort to hold back the clock and preserve some romantic idealized version of a pristine natural world, but for a rational attempt to understand the disturbed ecosystems that we have created and to manage them to support both humans and wildlife. I have no simple recipes for how to accomplish this. For the reasons given above, it will require the collaboration of basic scientists working to understand general patterns and processes and applied scientists willing to deal with the unique attributes of particular species and places. It will be a difficult, imprecise, error-plagued effort, and if we scientists, the public, or the decision-makers expect too much too soon, all are bound to be disappointed. It will require that we remain open-minded and flexible about, among other things, the ecological roles of invading species.

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