3

HUMAN INFLUENCE ON ANIMALS

Introduction

The range of impacts that humans, who now have the greatest biomass of any species, have had on animals, although large, can be grouped conveniently into five main categories: domestication, dispersal, extinction, expansion, and contraction. Humans have domesticated many animals, to the extent that, as with many plants, those animals depend on humans for their survival and, in some cases, for their reproduction. As with plants, people have helped to disperse animals deliberately, although many have also been dispersed accidentally, for the number of animals that accompany people without their leave is enormous, especially if we include the clouds of microorganisms that infest their land, food, clothes, shelter, domestic animals, and their own bodies. The extinction of animals by human predators has been extensive over the past 20,000 years, and in spite of recent interest in conservation continues at a high rate. In addition, the presence of humans has led to the contraction in the distribution and welfare of many animals (because of factors such as pollution), although in other cases human alteration of the environment and modification of competition has favored the expansion of some species, both numerically and spatially.

Domestication of animals

We have already referred briefly in Chapter 1 to one of the great themes in the study of human influence on nature: domestication. This has been one of the most profound ways in which humans have affected animals, for during the ten or eleven millennia that have passed since this process was initiated the animals that human societies have selected as useful to them have undergone major changes. Relatively few animal species have been domesticated in comparison with plant species, but for those that have been the consequences are so substantial that the differences between breeds of animals of the same species often exceed those between different species under natural conditions (Figure 3.1). A cursory and superficial comparison of the tremendous range of shapes and sizes of modern dog breeds (as, e.g., between a wolfhound

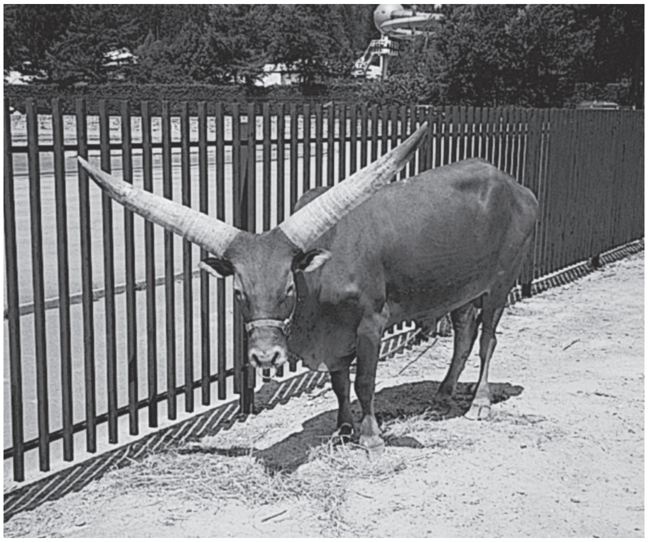

Figure 3.1 The consequences of domestication for the form of animals is dramatically illustrated by this large-horned but dwarf cow being displayed in a circus in Chamonix, France.

and a chihuahua) is sufficient to establish the extent of alteration brought about by domestication, and the speed at which domestication has accelerated the process of evolution. In particular humans have changed and enhanced the characteristics for which they originally chose to domesticate animals. For example, the wild ancestors of cattle gave no more than a few hundred milliliters of milk; today the best milk cow can yield up to 15,000 L of milk during its lactation period. Likewise, sheep have changed enormously (Ryder, 1966). Wild sheep have short tails, whereas modern domestic sheep have long tails, which may have arisen during human selection of a fat tail. Wild sheep also have an overall brown color, whereas domestic sheep tend to be mainly white. Moreover, the woolly undercoats of wild sheep have developed at the expense of bristly outer coats. With the ancestors of domestic sheep, wool (which served as protection for the skin and as insulation) consisted mainly of thick rough hairs and a small amount of down; the total weight of wool grown per year probably never reached 1 kg. The wool of present-day fine-fleeced sheep consists of uniform, thin down fibers and the total yearly weight may now reach 20 kg. Wild sheep also undergo a complete spring molt, whereas domestic sheep rarely shed wool.

Indeed, one of the most important consequences or manifestations of the domestication of animals consists of a sharp change in the seasonal biology. Whereas wild ancestors of domesticated beasts are often characterized by relatively strict seasonal reproduction and molting rhythms, most domesticated species can reproduce at almost any season of the year and tend not to molt to a seasonal pattern.

The most important center of animal domestication, shown in figure 1.6, was southwest Asia (cattle, sheep, goat, and pig) but other centers were important (e.g., the chicken in southeast Asia, the turkey in the Andes, and the horse in the Ukraine).

Dispersal and invasion of animals

Zoogeographers devote much time to dividing the world into regions with distinctive animal life – the great 'faunal realms' of Wallace and subsequent workers. This pattern of wildlife distribution evolved slowly over geologic time. The most striking dividing line between such realms is probably that between Australasia and Asia – **Wallace's Line**. Because of its isolation from the Asian landmass, Australasia developed a distinctive fauna characterized by its relative absence of placental mammals, its well-developed marsupials, and the egg-laying monotremes (echidna and the platypus).

Modern societies, by moving wildlife from place to place, consciously or otherwise, are breaking down these classic distinct faunal realms. Highly adaptable and dispersive forms are spreading, perhaps at the expense of more specialized organisms. Humans have introduced a new order of magnitude into distances over which dispersal takes place, and through the transport by design or accident of seeds or other propagules, through the disturbance of native plant and animal communities and of their habitat, and by the creation of new habitats and niches, the invasion and colonization by adventive species is facilitated.

Di Castri (1989) has identified three main stages in the process of biological invasions stimulated by human actions. In the first stage, covering several millennia up to about AD 1500, human historical events favored invasions and migrations primarily within the Old World. The second stage commenced about AD 1500, with the discovery, exploration, and colonization of new territories, and the initiation of 'the globalization of exchanges'. It shows the occurrence of flows of invaders from, to, and within the Old World. The

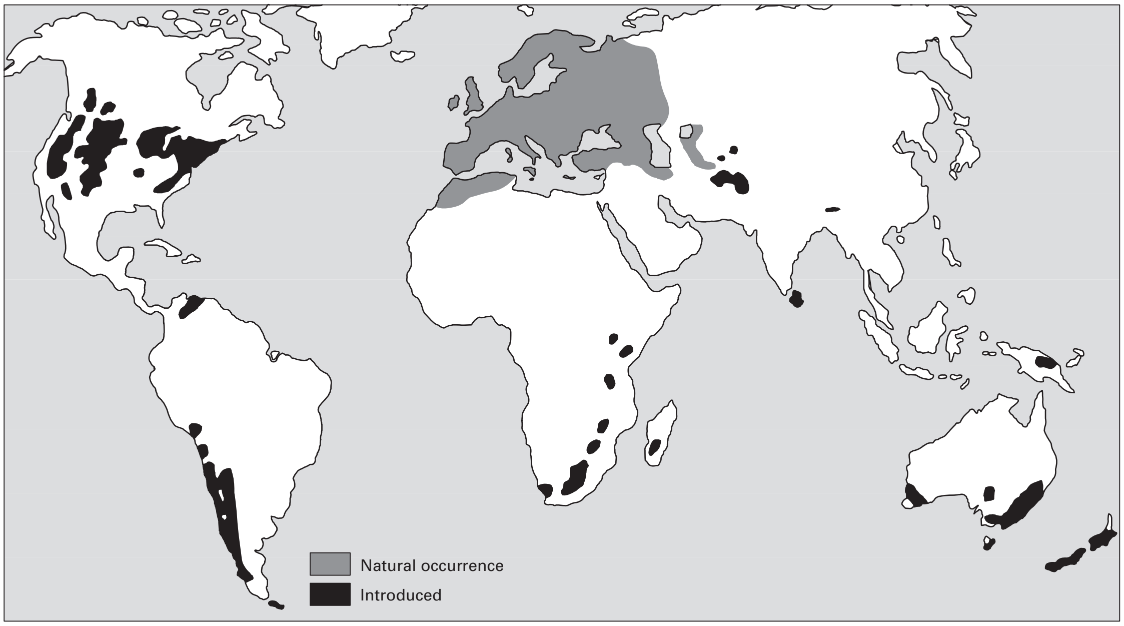

Figure 3.2 The original area of distribution of the brown trout and areas where it has been artificially naturalized (after MacCrimmon, in Illies, 1974, figure 3.2).

third stage, which covers only the last 100 to 150 years, sees an even more extensive 'multifocal globalization' and an increasing rate of exchanges. The Eurocentric focus has diminished.

Deliberate introductions of new animals to new areas have been carried out for many reasons (Roots, 1976): for food, for sport, for revenue, for sentiment, for control of other pests, and for aesthetic purposes. Such *deliberate* actions probably account, for instance, for the widespread distribution of trout (see Figure 3.2). There have, however, been many *accidental* introductions, especially since the development of ocean-going vessels. The rate is increasing, for whereas in the eighteenth century there were few ocean-going vessels of more than 300 tonnes, today there are thousands. Sea-borne trade now exceeds 5 billion tonnes per year and in 1998 much of it was carried in some 165 million containers. Many vessels dump ballast containing potentially invasive exotic species. Because of this, in the words of Elton (1958: 31), 'we are seeing one of the great historical convulsions in the world's fauna and flora.' Indeed, many animals are introduced with vegetable products, for 'just as trade followed the flag, so animals have followed the plants.' One of the most striking examples of the accidental introduction of animals given by Elton is the arrival of some chafer beetles, *Popillia japonica* (the Japanese beetle), in New Jersey in a consignment of plants from Japan. From an initial population of about one dozen beetles in 1916, the center of population grew rapidly outwards to cover many thousands of square kilometers in only a few decades (Figure 3.3).

A more recent example of the spread of an introduced insect in the Americas is provided by the Africanized honeybee, which is popularly known as the 'killer bee' (Rinderer et al., 1993). A number of these were brought to Brazil from South Africa in 1957 as an experiment and some escaped. Since then (Figure 3.4) they have moved northwards to Central America and Texas, spreading at a rate of 300–500 km per year, and competing with established populations of European honey bees. In 1998 they reached as far north as Nevada. Goulson (2003) reviews some of the adverse environmental effects of introduced bees, including their pollination of exotic weeds.

Some animals arrive accidentally with other beasts that are imported deliberately. In northern Australia, for instance, water buffalo were introduced (McKnight, 1971) and brought their own bloodsucking fly, a species which bred in cattle dung and transmitted an organism sometimes fatal to cattle. Australia's native dung beetles, accustomed only to the small sheep-like pellets of the grazing marsupials, could not tackle the large dung pats of the buffalo. Thus untouched pats

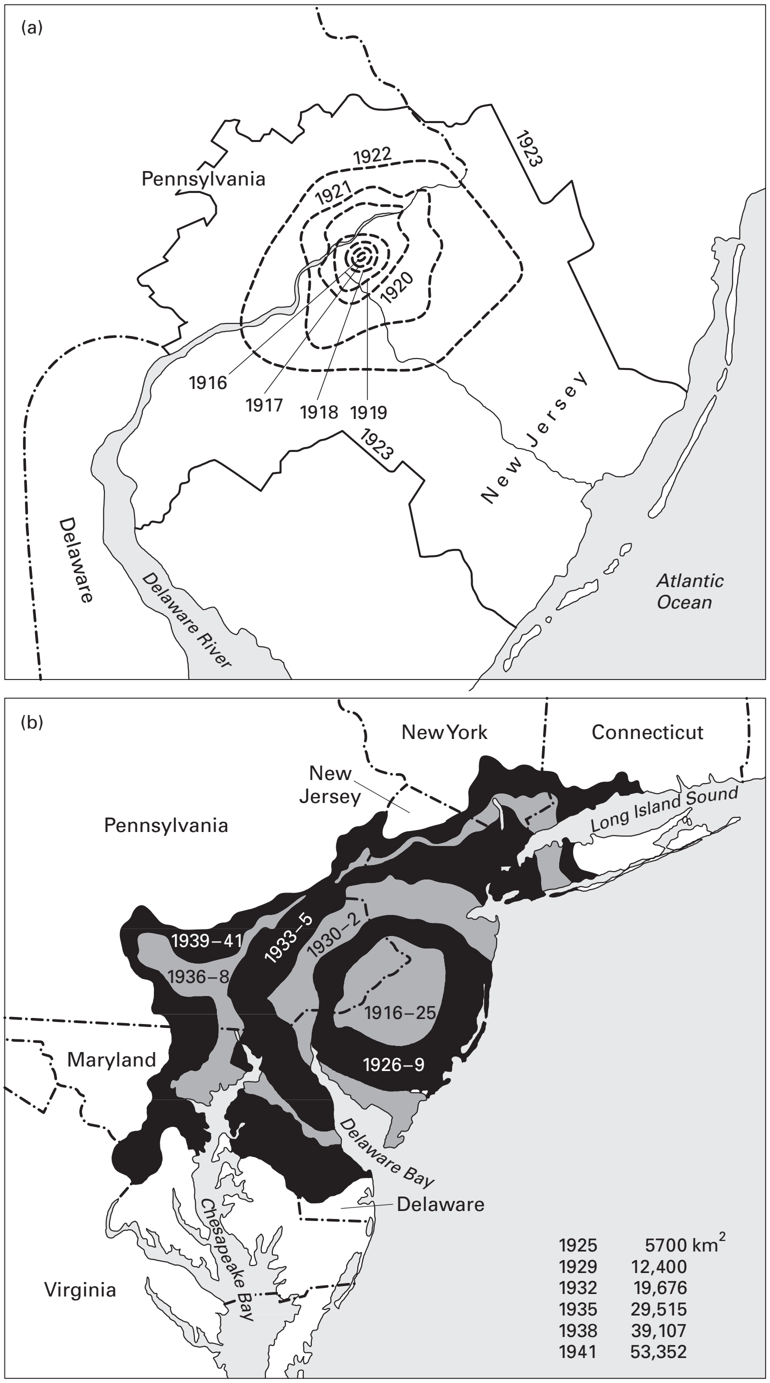

Figure 3.3 The spread of the Japanese beetle, *Popillia japonica*, in the eastern USA: (a) from its point of introduction in New Jersey, 1916–23 (after Elton, 1958, figure 14, and Smith and Hadley, 1926); (b) from its point of introduction to elsewhere, 1916–41 (after Elton, 1958, figure 15, and US Bureau of Entomology, 1941).

abounded and the flies were able to breed undisturbed. Eventually African dung beetles were introduced to compete with the flies (Roots, 1976). Indeed, animal invaders have had tragic consequences for the native Australian fauna and flora. Among the worst offenders are the rabbit, the fox, the feral pigs and goats, dogs, cats, mice, buffalo, camels, rats, cave toads, and various birds (Bomford and Hart, 2002). In neighboring New Zealand, Australian possums have become major pests.

While domesticated plants have, in most cases, been unable to survive without human help, the same is not so true of domesticated animals. There are a great

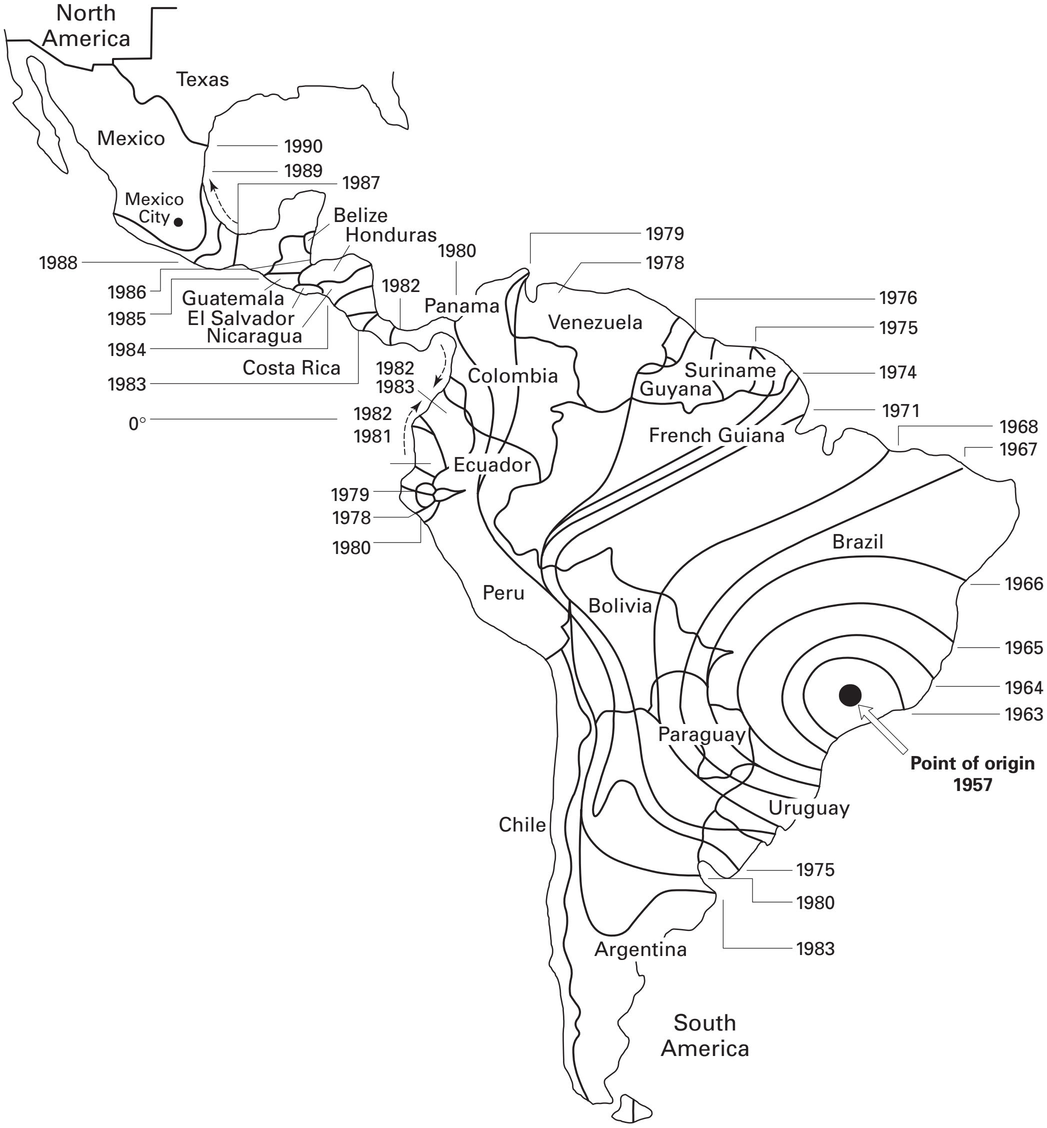

Figure 3.4 The spread of the Africanized honey bee in the Americas between 1957 (when it was introduced to Brazil) and 1990 (modified after Texas Agricultural Experiment Station, in *Christian science monitor*, September 1991).

many examples of cattle, horses (see, e.g., McKnight, 1959), donkeys, and goats which have effectively adapted to new environments and have virtually become wild (feral). Frequently feral animals have both ousted native animals and, particularly in the case of goats on ocean islands, caused desertification. Sometimes, however, introduced animals have spread so thoroughly and rapidly, and have led to such a change in the environment to which they were introduced, that they have sown the seeds of their own demise. Reindeer, for example, were brought from Lapland to Alaska in 1891–1902 to provide a new resource for the Eskimos, and the herds increased and spread to over half a million animals. By the 1950s, however, there was less than a twentieth of that number left, since the reindeer had been allowed to eat the lichen supplies that are essential to winter survival; as lichen grows very slowly their food supply was drastically reduced (Elton, 1958: 129).

The accidental dispersal of animals can be facilitated by means other than transport on ships or introduction with plants. This applies particularly to aquatic

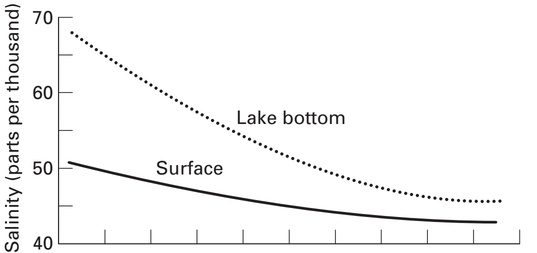

Figure 3.5 Decrease in the salinity of the Great Bitter Lake, Egypt, resulting from the intrusion of fresher water by way of the Suez Canal (after Wooster, 1969, with subsequent modification).

life, which can be spread through human alteration of waterways by methods such as canalization. Wooster (1969) gives the example of the way in which the construction of the Suez Canal has enabled the exchange of animals between the Red Sea and the eastern Mediterranean. Initially, the high salinity of the Great Bitter Lake acted to prevent movement, but the infusion of progressively fresher waters (Figure 3.5) through the Suez Canal has meant that this barrier has gradually become less effective. Some 39 Red Sea fish immigrants have now been identified in the Mediterranean, and they are especially important in the Levant basin, where they comprise about 12% of the fish population. Menacing jellyfish (*Rhopilema nomadica*) have invaded Levantine beaches (Spanier and Galil, 1991). This type of movement has recently been termed 'Lessepsian migration'. Similarly, the construction of the Welland Canal, linking the Atlantic with the Great Lakes of North America, has permitted similar movements with more disastrous consequences. Much of the native fish fauna has been displaced by alewife (*Alosa pseudoharengus*) through competition for food, and by the sea-lamprey (*Petromyzon marinum*) as a predator, so that once common Atlantic salmon (*Salmo salar*), lake trout (*Salvelinus namaycush*), and lake herring (*Leucichtys artedi*) have been nearly exterminated (Aron and Smith, 1971). The whole question of the presence and effects of exotic species in large lakes is reviewed by Hall and Mills (2000).

Can one make any generalizations about the circumstances that enable successful invasion by some exotic vertebrates and less successful invasion by others (Duncan et al., 2003)? Brown (1989) suggests that there may be 'five rules of biological invasions':

Rule 1
'Isolated environments with a low diversity of native species tend to be differentially susceptible to invasion.'
Rule 2
'Species that are successful invaders tend to be native to continents and to extensive, non-isolated habitats within continents.'
Rule 3
'Successful invasion is enhanced by similarity in the physical environment between the source and target areas.'
Rule 4
'Invading exotics tend to be more successful when native species do not occupy similar niches.'
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.'

Human influence on the expansion of animal populations

Although most attention tends to be directed towards the decline in animal numbers and distribution brought about by human agency, there are many circumstances where alterations of the environment and modification of competition has favored the expansion of some species. Such expansion is not always welcome or expected, as Marsh (1864: 34) appreciated:

> Insects increase whenever the birds which feed upon them disappear. Hence in the wanton destruction of the robin and other insectivorous birds, the *Bipes implumis*, the featherless biped, man, is not only exchanging the vocal orchestra which greets the rising sun for the drowsy beetle's evening drone, and depriving his groves and his fields of their fairest ornament, but he is waging a treacherous warfare on his natural allies.

Human actions, however, are not invariably detrimental, and even great cities may have effects on animal life which can be considered desirable or tolerable. This has been shown in the studies of bird populations in several urban areas. For example, Nuorteva (in Jacobs, 1975) examined the bird fauna in the city of Helsinki (Finland), in agricultural areas near rural houses, and in uninhabited forests (see Table 3.1). The city supported by far the highest biomass and the highest number of birds, but exhibited the lowest number of species and the lowest diversity. In the artificially

Table 3.1 Dependence of bird biomass and diversity on urbanization. Source: data from Nuorteva (1971) modified after Jacobs (1975, table 2)

	City (Helsinki)	*Near rural houses*	*Uninhabited forest*
Biomass (kg km^{-2})	213	30	22
No. of birds (km^{-2})	1089	371	297
Number of species	21	80	54
Diversity	1.13	3.40	3.19

created rural areas the number of species, and hence diversity, were much higher than in the uninhabited forest, and so was biomass. Altogether, human civilization appeared to have brought about a very significant increase of diversity in the whole area: there were 37 species in city and rural areas that were not found in the forest. Similarly, after a detailed study of suburban neighborhoods in west central California, Vale and Vale (1976) found that in suburban areas the number of bird species and the number of individuals increased with time. Moreover, when compared with the pre-suburban habitats adjacent to the suburbs, the residential areas were found to support a larger number of both species and individuals. Horticultural activities appear to provide more luxuriant and more diverse habitats than do pre-suburban environments.

Some beasts other than the examples of birds given here are also favored by urban expansion (Schmid, 1974). Animals that can tolerate disturbance, are adaptable, utilize patches of open or woodland-edge habitat, creep about inside buildings, tap people's food supply surreptitiously, avoid recognizable competition with humans, or attract human appreciation and esteem may increase in the urban milieu. For these sorts of reasons the northeast megalopolis of the USA hosts thriving populations of squirrels, rabbits, raccoons, skunks, and opossums, while some African cities are now frequently blessed with the scavenging attention of hyenas.

Jacobs (1975) provides another apposite example of how humans can increase species diversity inadvertently. The saline Lake Nakuru in Kenya before 1961 was not a particularly diverse ecosystem. There were essentially one or two species of algae, one copepod, one rotifer, corixids, notonectids, and some 500,000 flamingos belonging virtually to one species. In 1962, however, a fish (*Tilapia grahami*) was introduced in order to check mosquitoes. In the event it established itself as a major consumer of algae, and its numbers increased greatly. As a consequence, some 30 species of fish-eating birds (pelicans, anhingas, cormorants, herons, egrets, grebes, terns and fish-eagles) have colonized the area to make Lake Nakuru a much more diverse system. Nonetheless, such fish introductions are not without their potential ecological costs. In Lake Atitlan in Central America the introduction of the game fish *Micropterus salmoides* (largemouth bass) and *Pomoxis nigromaculatus* (black crappie), both voracious eaters, led to the diminution of local fish and crab populations. Similarly, the introduction to the Gatun Lake in the Panama Canal Zone in 1967 of the cichlid fish, *Cichla ocellaris* (a native of the Amazon River), led to the elimination of six of the eight previously common fish species within five years, and the tertiary consumer populations such as the birds, formerly dependent on the small fishes for food, appeared less frequently (Zaret and Paine, 1973).

Human economic activities may lead to a rise in the number of examples of a particular habitat which can lead to an expansion in the distribution of certain species, though often humans have prompted a contraction in the range of a particular species because of the removal or modification of its preferred habitat. In Britain the range of the little ringed plover (*Charadrius dubius*), a species virtually dependent on anthropogenic habitats, principally wet gravel and sand pits, greatly expanded as mineral extraction accelerated (see Figure 3.6). Indeed, it needs to be stressed that the changes of habitat brought about by urbanization, industry (Ratcliffe, 1974; Davis, 1976), and mining need not be detrimental.

Very often human activities do not lead to species diversity, but to important increases in numbers of individuals, by creating new and favorable environments. Two especially serious examples of this from the human point of view are the explosions in the prevalence of both mosquitoes and bilharzia snails as a result of the extension of irrigation.

One of the most remarkable examples of the consequences of creating new environments is provided by the European rabbit (*Oryctolagus cuniculus*). Introduced into Britain in early medieval times, and originally an inhabitant of the western Mediterranean lands, it was

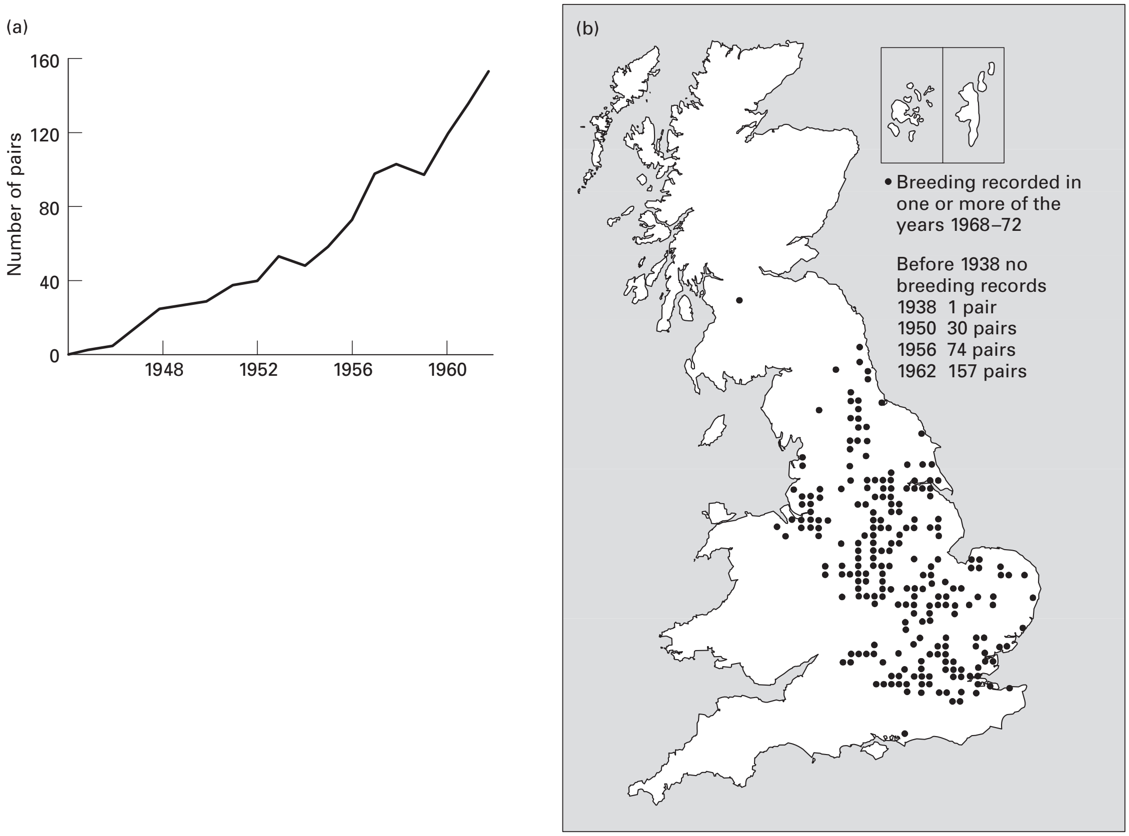

Figure 3.6 The changing range of the little ringed plover (*Charadrius dubius*): (a) the increase in the number summering in Britain (after Murton, 1971, figure 6); (b) the increase in the range, related to habitat change, especially as a result of the increasing number of gravel pits (after Nature Conservancy Council, 1977, figure 11).

kept for food and fur in carefully tended warrens. Agricultural improvements, especially to grassland, together with the increasing decline in the numbers of predators such as hawks and foxes, brought about by game-guarding landlords (Sheail, 1971), enabled the rabbit to become one of the most numerous of mammals in the British countryside. By the early 1950s there were 60–100 million rabbits in Britain. Frequently, as many contemporary reports demonstrated, it grazed the land so close that in areas of light soil, like the Breckland of East Anglia or in coastal dune areas, wind erosion became a serious problem. Similarly, the rabbit flourished in Australia, especially after the introduction of the merino sheep, which created favorable pasturelands. Erosion in susceptible lands such as the Mallee was severe. Both in England and Australia an effective strategy developed to control the rabbit was the introduction of a South American virus, *Myxoma*.

Some of the familiar British birds have benefited from agricultural expansion. Formerly, when Britain was an extensively wooded country, the starling (*Sturnus vulgaris*) was a rare bird. The lapwing (*Vanellus vanellus*) is yet another component of the grassland fauna of central Europe which has benefited from agriculture and the creation of open country with relatively sparse vegetation (Murton, 1971). There is also a large class of beasts which profit so much from the environmental conditions wrought by humans that they become very closely linked to them. These animals are often referred to as **synanthropes**. Pigeons and sparrows now form permanent and numerous populations in almost all the large cities of the world; human food supplies are the food supplies for many synanthropic rodents (rats and mice); a once shy forest-bird, the blackbird (*Turdus merula*), has in the course of a few generations become a regular and bold inhabitant of

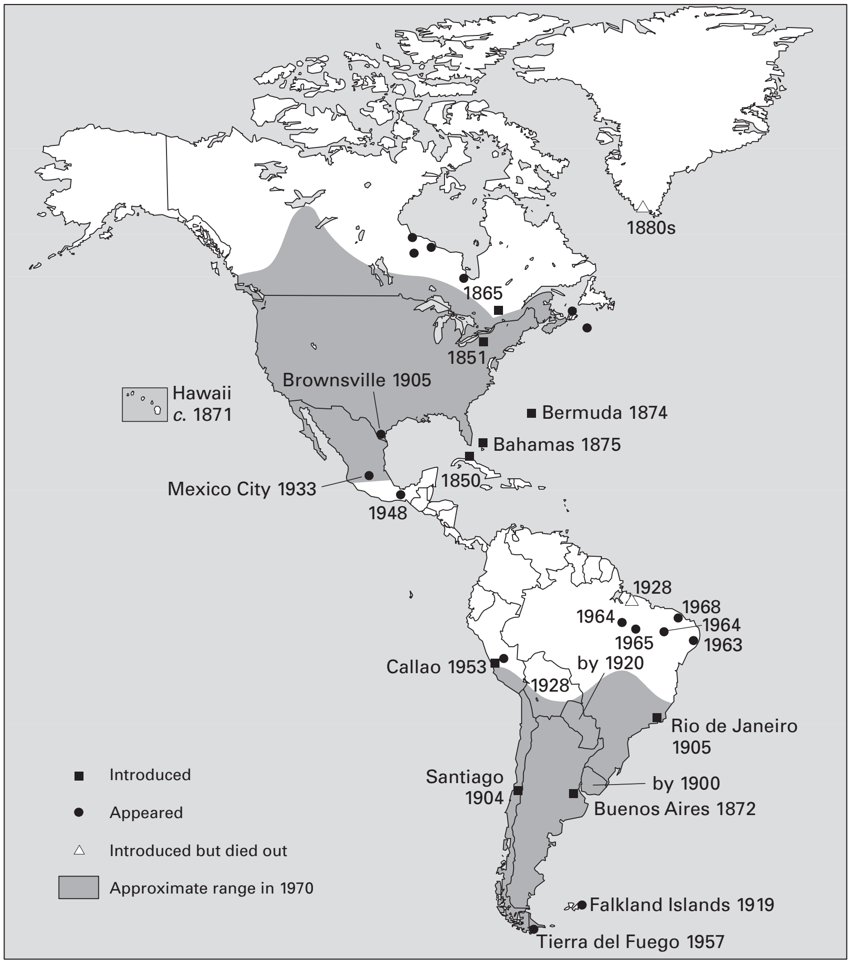

Figure 3.7 The spread of the English house sparrow in the New World (after Doughty, 1978: 14).

many gardens in the UK; and the squirrel (*Sciurus vulgaris*) in many places now occurs more frequently in parks than in forests (Illies, 1974: 101). The English house sparrow (*Passer domesticus*), a familiar bird in towns and cities, currently occupies approximately one-quarter of Earth's surface, and over the past 100 years it has doubled the area that it inhabits as settlers, immigrants, and others have carried it from one continent to another (Figure 3.7), although recently in Britain, for reasons that are not clear, it has suffered a decline in numbers. It is found around settlements both in Amazonia and the Arctic Circle (Doughty, 1978). The marked increase in many species of gulls in temperate regions over recent decades is largely attributable to their growing utilization of food scraps on refuse tips. This is, however, something of a mixed blessing, for most of the gull species which feed on urban rubbish dumps breed in coastal areas, and there is now good evidence to show that their greatly increased numbers are threatening other less common species, especially the terns (*Sterna* spp.). It may seem incongruous that the niches for scavenging birds which exploit rubbish tips should have been filled by sea birds (Murton, 1971), but the gulls have proved ideal replacements for the kites which humans had removed, as they have the same ability to watch out for likely food sources from aloft and then to hover and plunge when they spy a suitable meal.

Most of the examples given so far to illustrate how human actions can lead to expansion in the numbers and distributions of certain animal species have been used to make the point that such expansion frequently

Table 3.2 Introduced mammals in Britain. Source: from Jarvis (1979: 188, table 1)

Species	*Date of introduction of present stock*	*Reason for introduction*
House mouse *Mus musculus*	Neolithic?	Accidental
Wild goat *Capra hircus*	Neolithic?	Food
Fallow deer *Dama dama*	Roman or earlier	Food, sport
Domestic cat *Felis catus*	Early Middle Ages	Ornament, pest control
Rabbit *Oryctolagus cuniculus*	Mid- to late twelfth century	Food, sport
Black rat *Rattus rattus*	Thirteenth century?	Accidental
Brown rat *Rattus norvegicus*	Early eighteenth century (1728–9)	Accidental
Sika deer *Cervus nippon*	1860	Ornament
Grey squirrel *Sciurus carolinensis*	1876	Ornament
Indian muntjak *Muntiacus muntjak*	1890	Ornament
Chinese muntjak *Muntiacus reevesi*	1900	Ornament
Chinese water deer *Hydropetes inermis*	1900	Ornament
Edible dormouse *Glis glis*	1902	Ornament
Musk rat *Ondatra zibethica*	1929–1937	Fur
Coypu *Myocastor coypus*	1929	Fur
Mink *Mustela vison*	1929	Fur
Bennett's wallaby *Macropus rufogriseus bennetti*	1939 or 1940	Ornament
Reindeer *Rangifer tarandus*	1952	Herding, ornament
Himalayan (Hodgson's) porcupine *Hystrix hodgsoni*	1969	Ornament
Crested porcupine *Hystrix cristata*	1972	Ornament
Mongolian gerbil *Meriones unguiculatus*	1973	Ornament

occurs as an incidental consequence of human activities. There are, of course, many ways in which people have intentionally and effectively promoted the expansion of particular species (Table 3.2 presents data for some introduced mammals in Britain). This may sometimes be done deliberately to reduce the numbers of a species that have expanded as an unwanted consequence of human actions. Perhaps the best known example of this is biological control using introduced predators and parasites. Thus an Australian insect, the cottony-cushion scale, *Icerya purchasi*, was found in California in 1868. By the mid-1880s it was effectively destroying the citrus industry, but its ravages were quickly controlled by deliberately importing a parasitic fly and a predatory beetle (the Australian ladybird) from Australia. Because of the uncertain ecological effects of synthetic pesticides, such biological control has its attractions but the importation of natural enemies is not without its own risks. For example, the introduction into Jamaica of mongooses to control rats led to the undesirable decimation of many native birds and small land mammals.

One further calculated method of increasing the numbers of wild animals, of conserving them, and of gaining an economic return from them, is game cropping. In some circumstances, because they are better adapted to, and utilize more components of, the environment, wild ungulates provide an alternative means of land use to domestic stock. The exploitation of the saiga antelope, *Saiga tatarica*, in the Soviet Union is the most successful story of this kind (Edington and Edington, 1977). Hunting, much overdone because of the imagined medical properties of its horns, had led to its near demise, but this was banned in the 1920s and a system of controlled cropping was instituted. Under this regime (which produces appreciable quantities of meat and leather) total numbers have risen from about 1000 to over 2 million in the 1970s, and in the process the herds have reoccupied most of their original range. Since the break up of the Soviet Union, however, previously successful conservation schemes have suffered from a shortage of funding and high levels of poverty and unemployment have encouraged poaching.

Causes of animal contractions and declines: pollution

The extreme effect of human interference with animals is extinction, but before that point is reached humans may cause major contractions in both animal numbers and animal distribution. This decline may be brought about partly by intentional killings for subsistence and commercial purposes, but much wildlife decline occurs indirectly (Doughty, 1974), for example, through pollution (Holdgate, 1979; Waldichuk, 1979), habitat change or loss, and competition from invaders.

Particular concern has been expressed about the role of certain pesticides in creating undesirable and unexpected changes. The classic case of this concerns dichlorodiphenyltrichloroethane (DDT) and related substances. These were introduced on a worldwide basis after the Second World War and proved highly effective in the control of insects such as malarial mosquitoes. However, evidence accumulated that DDT was persistent, capable of wide dispersal, and reached high levels of concentration in certain animals at the top **trophic** levels. The tendency for DDT to become more concentrated as one moves up the food chain is illustrated further by the data in Table 3.3(c). Levels of DDT in river and estuary waters may be low, but the zooplankton and shrimps contain higher levels, the fish that feed on them higher levels still, while fish-eating birds have the highest levels of all.

Dichlorodiphenyltrichloroethane has a major effect on sea birds. Their eggshells become thinned to the extent that reproduction fails in fish-eating birds. Similar correlations between eggshell thinning and DDT residue concentrations have been demonstrated for various raptorial land-birds. The bald eagle (*Haliaeetus leucocephalus*), peregrine falcon (Figure 3.8) (*Falco peregrinus*), and osprey (*Pandion haliaetus*) all showed

Table 3.3 Examples of biological magnification

(a) Enrichment factors for the trace element compositions of shellfish compared with the marine environment. Source: Merlini (1971) in King (1975: 303, table 8.8)

Element	*Enrichment factor*		
	Scallops	*Oysters*	*Mussels*
Ag	23,002	18,700	330
Cd	260,000	318,000	100,000
Cr	200,000	60,000	320,000
Cu	3000	13,700	3000
Fe	291,500	68,200	196,000
Mn	55,000	4000	13,500
Mo	90	30	60
Ni	12,000	4000	14,000
Pb	5300	3300	4000
V	4500	1500	2500
Zn	28,000	110,300	9100

(b) Mean methyl mercury concentrations in organisms from a contaminated salt marsh. Source: Gardner et al. (1978) in Bryan (1979)

Organism	*Parts per million*
Sediments	< 0.001
Spartina	< 0.001–0.002
Echinoderms	0.01
Annelids	0.13
Bivalves	0.15–0.26
Gastropods	0.25
Crustaceans	0.28
Fish muscle	1.04
Fish liver	1.57
Mammal muscle	2.2
Bird muscle	3.0
Mammal liver	4.3
Bird liver	8.2

(c) The concentration of dichlorodiphenyltrichloroethane (DDT) in the food chain. Source: King (1975: 301, table 8.7)

Source	*Parts per million*
River water	0.000003
Estuary water	0.00005
Zooplankton	0.04
Shrimps	0.16
Insects – Diptera	0.30
Minnows	0.50
Fundulus	1.24
Needlefish	2.00
Tern	2.80–5.17
Cormorant	26.40
Immature gull	75.50

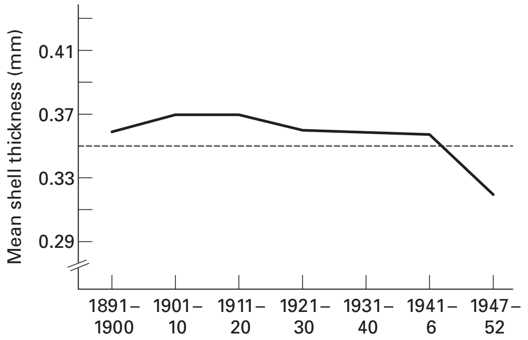

Figure 3.8 Changing thickness of peregrine falcon eggshells versus time, associated with dichlorodiphenyltrichloroethane (DDT) use since the Second World War (modified after Hickey and Anderson, 1968).

decreases in eggshell thickness and population decline from 1947 to 1967, a decline which correlated with DDT usage and subsequent reproductive and metabolic effects upon the birds (Johnston, 1974).

Another example serves to make the same point about the 'magnification' effects associated with pesticides (Southwick, 1976: 45–6). At Clear Lake in California, periodic appearances of large numbers of gnats caused problems for tourists and residents. An insecticide, dichlorodiphenyldichloroethane (DDD), was applied at a low concentration (up to 0.05 ppm) and killed 99% of the larvae. Following the application of DDD, western grebes (*Alchmorphorus occidentalis*) were found dead, and tissue analysis showed concentrations of DDD in them of 1600 ppm, representing a concentration of 32,000 times the application rate. The DDD had accumulated in the insect-eating fish at levels of 40–2500 ppm and the grebes feeding on the fish received lethal doses of the pesticide. There are also records elsewhere of trout reproduction ceasing when DDT levels build up (Chesters and Konrad, 1971).

However, appreciation of the undesirable side effects of DDD and DDT brought about by ecological concentration has led to severe controls of their use. For example, DDT reached a peak in terms of utilization in the USA in 1959 (35×10^6 kg) and by 1971 was down to 8.1×10^6 kg. The monitoring of birds in Florida over the same period indicated a parallel decline in the concentration of DDT and its metabolites (DDD and dichlorodiphenyldichloroethylene – DDE) in their fat deposits (Johnston, 1974). Other substances are also capable of concentration. For example, heavy metals and methyl mercury may build up in marine organisms, and filter feeders such as shellfish have a strong tendency to concentrate the metals from very dilute solutions, as is clear in Table 3.3(a and b).

It is possible, however, that the importance of biological accumulation and magnification has been overstated in some textbooks. G. W. Bryan (1979) reviewed the situation and noted that, although the absorption of pollutants from foods is often the most important route for bioaccumulation, and transfer along food chains certainly occurs, this does not automatically mean that predators at high trophic levels will always contain the highest levels. He wrote (p. 497):

> although, for a number of contaminants, concentrations in individual predators sometimes exceed those of their prey, when the situation overall is considered only the more persistent organochlorine pesticides, such as DDT and its metabolites and methyl mercury, show appreciable signs of being biologically magnified as a result of food-chain transfer.

Oil pollution is a serious problem for marine and coastal fauna and flora (Figure 3.9), although some of it derives from natural seeps (Blumer, 1972; Landes, 1973). Sea birds are especially vulnerable since oil clogs their feathers, while the ingestion of oil when birds attempt to preen themselves leads to enteritis and other complaints. Local bird populations may be seriously diminished although probably no extinction has resulted (Bourne, 1970). Fortunately, although oil is toxic it becomes less so with time, and the oil spilt from the *Torrey Canyon* in March 1967 was almost biologically inert when it was stranded on the Cornish beaches (Cowell, 1976). There are 'natural' oil-degrading organisms in nature. Much of the damage caused to marine life as a result of this particular disaster was caused not by the oil itself but by the use of 2.5 million gallons of detergents to disperse it (Smith, 1968).

It is possible that oil spills pose a particular risk in cold areas, for **biodegradation** processes achieved by microbes appear to be slow. This is probably because of a combination of low temperatures and limited availability of nitrogen, phosphorus, and oxygen. The last of these is a constraint because, compared with temperate ecosystems, arctic tundra and coastal ecosystems are relatively stagnant – ice dampens re-aeration due to wave action in marine ecosystems, while standing water in tundra soils limits inputs of oxygen to them. Detailed reviews are provided in Engelhardt (1985).

There is far less information available on the effects of oil spills in freshwater environments, although they undoubtedly occur. Freshwater bodies have certain characteristics which, compared with marine environments, tend to modify the effects of oil spills. The most important of these are the smaller and shallower dimensions of most rivers, streams, and lakes, which means that dilution and spreading effects are not as vigorous and significant in reducing surface slicks as would be the case at sea. In addition, the confining dimensions of ponds and lakes are likely to cause organisms to be subjected to prolonged exposure to dissolved and dispersed hydrocarbons. Information on this problem is summarized in Vandermeulen and Hrudey (1987).

Figure 3.9 Oil spills are generally perceived as a major cause of pollution on coastlines. In January 1993 the tanker *Braer* ran aground on the Shetland Isles (Scotland) and large quantities of oil were liberated, causing some distress and mortality among sea birds.

Figure 3.10 Corals reefs are wonderfully attractive, diverse and productive ecosystems that are subjected to a whole series of threats. At Sharks Bay, on the Red Sea in Egypt, tourists are encouraged not to damage the coral reef offshore by avoiding trampling on the coral.

One particular type of aquatic ecosystem where pollution is an increasingly serious problem is the coral reef (Figure 3.10) (see Kuhlmann, 1988). Coral reefs are important because they are among the most diverse, productive, and beautiful communities in the world. Although they only cover an area of less than 0.2% of the world's ocean beds, up to one-quarter of all marine species and one-fifth of known marine fish species live in coral reef ecosystems (World Resources Institute, 1998: 253). They also provide coastal protection, opportunities for recreation, and potential sources of substances such as drugs. Accelerated sedimentation resulting from poor land management (Nowlis et al., 1997), together with dredging, is probably responsible for more damage to reef communities than all the other forms of human insult combined, for suspended sediments restrict the light penetration necessary for coral growth. Also, the soft, shifting sediments may not favor colonization by reef organisms. Sewage is the second worst form of stress to which coral reefs are exposed, for oxygen-consuming substances in sewage result in reduced levels of oxygen in the water of lagoons. The detrimental effects of oxygen starvation are compounded by the fact that sewage may cause nutrient enrichment to stimulate algal growth, which in turn can overwhelm coral. Poor land management can also cause salinity levels to be reduced below the level of tolerance of reef communities as a consequence of accelerated runoff of freshwater from catchments draining into lagoons. One of the reasons why all these stresses may be especially serious for reefs, is that corals live and grow for several decades or more, so that it can take a long time for them to recover from damage.

An interesting example of the role of sedimentation in damaging reef health is provided by geochemical studies of long-lived corals from Australia's Great Barrier Reef (McCulloch et al., 2003). These showed that since 1870 and the start of European settlement in its catchment the Burdekin River has carried five to ten times more sediment to the reef than it did previously.

Since the late nineteenth century it has been clear that industrial air pollution has had an adverse effect on domestic animals, but there is less information about its influence on wildlife. Nonetheless, there is some evidence that it does affect wild animals (Newman, 1979). Arsenic emissions from silver foundries are known to have killed deer and wild rabbits in Germany; sulfur emissions from a pulp mill in Canada are known to have killed many song-birds; industrial fluorosis has been found in deer living in the USA and Canada; asbestosis has been found in free-living baboons and rodents in the vicinity of asbestos mines in South Africa; and oxidants from air pollution are recognized causes of blindness in bighorn sheep in the San Bernadino Mountains near Los Angeles in California.

In Britain considerable concern has arisen over the effects of lead poisoning on wildlife, particularly on wildfowl. Poisoning occurs in swans and mallards, for example, when they feed and seek grit, since they ingest spent shotgun pellets or discarded anglers' weights in the process. Such pellets are eroded in the bird's gizzard and the absorbed lead causes a variety of adverse physiological effects that can result in death: damage to the nervous system, muscular paralysis, anemia, and liver and kidney damage (Mudge, 1983).

Soil erosion, by increasing stream **turbidity** (another type of pollution), may adversely affect fish habitats (Ritchie, 1972). The reduction of light penetration inhibits photosynthesis, which in turn leads to a decline in food and a decline in carrying capacity. Decomposition of the organic matter, which is frequently deposited with sediment, uses dissolved oxygen, thereby reducing the oxygen supply around the fish; sediment restricts the emergence of fry from eggs; and turbidity reduces the ability of fish to find food (though conversely it may also allow young fish to escape predators).

Turbidity has also been increased by mining waste, by construction (Barton, 1977), and by dredging. In the case of some of the Cornish rivers in china-clay mining areas, river turbidities reach 5000 mg L^{-1} and trout are not present in streams so affected. Indeed, the non-toxic turbidity tolerances of river fish are much less than that figure. Alabaster (1972), reviewing data from a wide range of sources, believes that in the absence of other pollution fisheries are unlikely to be harmed at chemically inert suspended sediment concentrations of less than 25 mg L^{-1}, that there should be good or moderate fisheries at 25–80 mg L^{-1}, that good fisheries are unlikely at 80–400 mg L^{-1} and that at best only poor fisheries would exist at more than 400 mg L^{-1}.

Habitat change and animal decline

Land use and land cover changes, including the conversion of natural ecosystems to cropland (Ramankutty and Foley, 1999), have so modified habitats that animal declines have ensued. Elsewhere ancient and diverse anthropogenic landscapes have themselves been modified by modern agricultural intensification. Good reviews of changes in biodiversity are provided by Heywood and Watson (1995) and Chapin et al. (2001). Certainly, many species have lost a very large part of their natural ranges as a result of human activities, and a study of historical and present distributions of 173 declining mammal species from six continents has indicated that these species have collectively lost over 50% of their historic range area (Ceballos and Ehilich, 2002).

One of the most important habitat changes in Britain has been the removal of many of the hedgerows that form the patchwork quilt so characteristic of large tracts of the country (Sturrock and Cathie, 1980). Their removal has taken place for a variety of reasons: to create larger fields, so that larger machinery can be employed and so that it spends less time turning; because as farms are amalgamated boundary hedges may become redundant; because as farms become more specialized (e.g., just arable) hedges may not be needed to control stock or to provide areas for lambing and calving; and because drainage improvements may be more efficiently executed if hedges are absent. In 1962 there were almost 1 million kilometers of hedge in Britain, probably covering the order of 180,000 hectares,

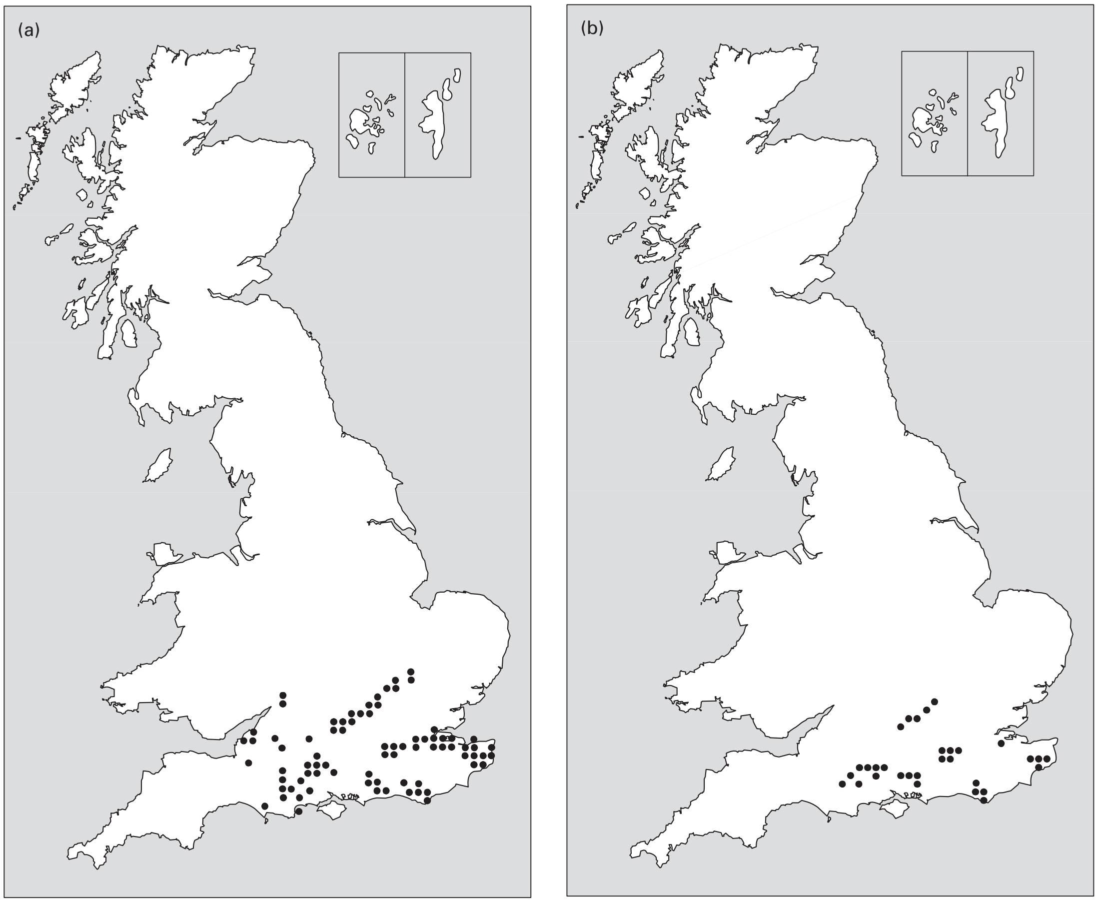

Figure 3.11 Reduction in the range of the silver-spotted skipper butterfly (*Hesperia comma*) as a result of the reduction in the availability of the chalk downland and limestone pastures upon which it depends. (a) Distribution prior to 1960 (after Nature Conservancy Council, 1977, figure 3.8). (b) Distribution in the late 1990s (from data provided by National Biodiversity Network).

an area greater than that of the national nature reserves. Bird numbers and diversity are likely to be severely reduced if the removal of hedgerows continues, for most British birds are essentially of woodland type and, since woods only cover about 5% of the land surface of Britain, depend very much on hedgerows (Moore et al., 1967).

Other types of habitat have also been disappearing at a fast rate with the agricultural changes of recent years (Nature Conservancy Council, 1977). For example, the botanical diversity of old grasslands is often reduced by replacing the lands with grass leys or by treating them with selective herbicides and fertilizers; this can mean that the habitat does not contain some of the basic requirements essential for many species. One can illustrate this by reference to the larva of the common blue butterfly (*Polyommatus icarus*) which feeds upon bird-foot trefoil (*Lotus corniculatus*). This plant disappears when pasture is ploughed and converted into a ley, or when it is treated with a selective herbicide. Once the plant has gone the butterfly vanishes too because it is not adapted to feeding on the plants grown in the ley of improved pasture. Figure 3.11 illustrates the way in which the distribution of the silver-spotted skipper butterfly (*Hesperia comma*) has contracted with the diminished availability of chalk downland and limestone pastures upon which it depends. Likewise, the large blue butterfly (*Maculinea arion*) has decreased in Britain. Its larvae live solely on the wild thyme (*Thymus druccei*), a plant that thrives on close-cropped grassland. Since the decimation of the rabbit by myxomatosis, conditions for the thyme

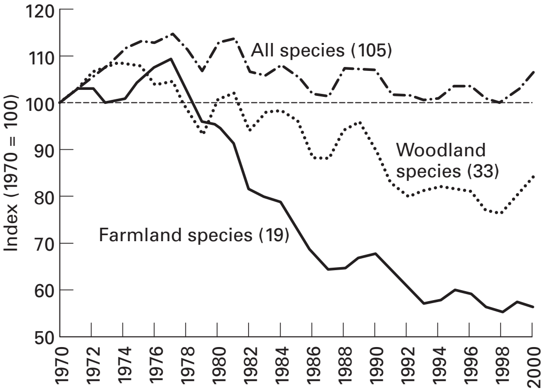

Figure 3.12 Population of wild birds in the UK, 1970–2000 (based on data from UK Department for Environment Food and Rural Affairs (Defra), 2003).

Table 3.4 Decline in farmland birds in Britain between 1972 and 1996 as shown by the Common Birds Census. Source: http://www.jncc.gov.uk/species/Birds/c0c_98.htm (accessed 15 October 2003)

Species	*% decline*
Corn bunting	74
Grey partridge	78
Tree sparrow	87
Lapwing	42
Bullfinch	62
Song thrush	66
Turtle dove	62
Linnet	40
Skylark	60
Spotted flycatcher	78
Blackbird	33

have been less favorable so that both thyme and the large blue butterfly have declined.

The replacement of natural oak-dominated woodlands in Britain by conifer plantations, another major land-use change of recent decades, also has its implications for wildlife. It has been estimated that where this change has taken place the number of species of birds found has been approximately halved (Figure 3.12). Likewise the replacement of upland sheep walks with conifer plantations has led to a sharp decline in raven numbers in southern Scotland and northern England. The raven (*Corvus corax*) obtains much of its carrion from open sheep country (Marquiss et al., 1978). Other birds that have suffered from planting moorland areas with forest plantations are miscellaneous types of wader, golden eagles, peregrine falcons, and buzzards (Grove, 1983).

Agricultural intensification on British farms also appears to have had a deleterious effect on species of farmland bird, many of which have shown a downward trend in numbers over the past three decades (Table 3.4). This is because of habitat changes – lack of fallows, less mixed farming, new crops, modern farm management, biocide use, hedgerow removal, etc. (Fuller et al., 1991).

On a global basis the loss of **wetland** habitats (Figure 3.13) (marshes, bogs, swamps, fens, mires, etc.) is a cause of considerable concern (Maltby, 1986; Williams, 1990). In all, wetlands cover about 6% of Earth's surface (not far short of the total under tropical rain forest), and so they are far from being trivial, even though they tend to occur in relatively small patches. However, they also account for about one-quarter of Earth's total net primary productivity, have a very diverse fauna and flora, and provide crucial wintering, breeding, and refuge areas for wildlife. According to some sources, the world may have lost half its wetlands since 1900, and the USA alone has lost 54% of its original wetland area, primarily because of agricultural developments. There are, however, other threats, including drainage, dredging, filling, peat removal, pollution, and **channelization**.

Figure 3.13 The Okavango Swamps in Botswana are an example of an important wetland habitat that is home to many species of plant and animal. Were the waters that drain into it to be diverted, an ecological and aesthetic tragedy would result.

In Europe and the USA 90% of riverine flood plains have been gravely and extensively modified as habitats and in ecological terms have been described as 'functionally extinct' (Tockner and Stanford, 2002).

Other causes of animal decline

One could list many other indirect causes of wildlife decline. Vehicle speed, noise, and mobility upset remote and sensitive wildlife populations, and this problem has intensified with the rapid development in the use of off-road recreation vehicles. The effects of roads are becoming ever more pervasive as a result of increasing traffic levels, vehicle speed, and road width, and a new subdiscipline of road ecology has emerged (Sherwood et al., 2002; Forman et al., 2003). A fine-meshed road network is a highly effective cause of habitat isolation, acting as a series of barriers to movement, particularly of small, cover-loving animals. As Oxley et al. (1974) have put it, 'a four-lane divided highway is as effective a barrier to the dispersal of small forest mammals as a body of fresh water twice as wide.' This barrier effect results from a variety of causes (Mader, 1984): roads interrupt microclimatic conditions; they are a broad band of emissions and disturbances; they are zones of instability due to cutting and spraying, etc.; they provide little cover against predators; and they subject animals to death and injury by moving wheels. Leisure activities in general may create problems for some species (Speight, 1973). A survey of the breeding status of the little tern (*Sterna albifrons*) in Britain gave a number of instances of breeding failure by the species, apparently caused by the presence of fishermen and bathers on nesting beaches. The presence of even a few people inhibited the birds from returning to their nests. In like manner, species building floating nests on inland waters, such as great crested grebes (*Podiceps cristatus*), are very prone to disturbance by water-skiers and powerboats.

New types of construction can cause problems. As Doughty (1974) has remarked '"wirescapes", tall buildings, and towers can become to birds what dams, locks, canals and irrigation ditches are to the passage of fish.' The construction of canals can cause changes in aquatic communities. Likewise turbines associated with hydroelectric schemes can cause numerous fish deaths, either directly through ingesting them, or through gas-bubble disease. This resembles the 'bends' in divers and is produced if a fish takes in water supersaturated with gases. The excess gas may come out of solution as bubbles, which can lodge in various parts of the fish's body causing injury or death. Supersaturation of water with gas can be produced in turbines or when a spillway plunges into a deep basin (Baxter, 1977).

It might also be thought that human use of fire could be directly detrimental to animals, though the evidence is not conclusive. Many forest animals appear to be able to adapt to fire, and fire also tends to maintain habitat diversity. Thus, after a general review of the available ecological literature Bendell (1974) found that fires did not seem to produce as much change in birds or small mammals as one might have expected. Some of his data are presented in Table 3.5. The amount of change is fairly small, although some increase in species diversities and animal densities is evident. Indeed Vogl (1977) has pointed to the diversity of fauna associated with fire-affected ecosystems (p. 281):

> Birds and mammals usually do not panic or show fear in the presence of fire, and are even attracted to fires and smoking or burned landscapes . . . The greatest arrays of higher animal species, and the largest numbers per unit area, are associated with fire-dependent, fire-maintained, and fire-initiated ecosystems.

Purposeful hunting, particularly when it involves modern firearms, means that the distribution of many animal species has become smaller very rapidly (Figure 3.14). This is clearly illustrated by a study of the North American bison (Figure 3.15), which on the eve of European colonization still had a population of some 60 million in spite of the presence of a small Indian population. By 1850 only a few dozen examples of bison still survived, though conscious protective and conservation measures have saved it from extinction.

Animals native to remote ocean islands have been especially vulnerable since many have no flight instinct. They also provided a convenient source of provisions for seafarers. Thus the last example of the dodo (*Raphus cucullatus*) was slaughtered on Mauritius in 1681 and the last Steller's sea cow (*Hydrodamalis gigas*) was killed on Bering Island in 1768 (Illies, 1974: 96). The land-birds, which are such a feature of coral atoll ecosystems, rapidly become extinct when cats, dogs, and rats are introduced. The endemic flightless rail of Wake Island, *Rallus wakensis*, became extinct during

Table 3.5 Environmental effects of burning
(a) Change in number of species of breeding birds and small mammals after fire

	Foraging zone	*Before fire*	*After fire*	*Gained (%)*	*Lost (%)*
Birds	Grassland and shrub	48	v62	38	8
	Tree trunk	25	26	20	16
	Tree	63	58	10	17
	Totals	136	146	21	14
Small mammals	Grassland and shrub	42	45	17	10
	Forest	16	14	13	25
	Totals	58	59	16	14

(b) Change in density and trend of population of breeding birds and small mammals after fire

	Foraging zone	*Density (%)*			*Trend (%)*		
		Increase	*Decrease*	*No change*	*Increase*	*Decrease*	*No change*
Birds	Grassland and shrub	50	9	41	24	10	66
	Tree trunk	28	16	56	4	8	88
	Tree	24	19	57	6	6	88
	Totals	35	15	50	12	8	80
Small mammals	Grassland and shrub	24	13	63	20	5	75
	Forest	23	42	35	0	11	89
	Totals	23	25	52	14	1	80

Figure 3.14 A major cause of animal decline is trapping. Here we see a sample of the many snares that have been found in a game reserve in Swaziland, southern Africa.

the prolonged siege of the island in the Second World War, and the flightless rail of Laysan, *Porzanula palmeri*, is also now extinct. Seabirds are more numerous on the atolls, but many colonies of terns, noddies, and boobies have been drastically reduced by vegetation clearance and by introduced rats and cats in recent times (Stoddart, 1968). Other atoll birds, including the albatross, have been culled because of the threat they pose to aircraft using military airfields on the islands. Some birds have declined because they are large, vulnerable, and edible (Feare, 1978).

The fish resources of the oceans are still exploited by hunting and gathering techniques, and about 95 million tonnes of fish are caught in the world each year, a more than fivefold increase since 1950. The world catch may have peaked, however, for some major fisheries have collapsed as a result of unsustainable exploitation (Hilborn et al., 2003). Chronic overfishing is a particular problem in shallow marginal seas (e.g., the North Sea) and in the vicinity of coral reefs, where the removal of herbivorous fish can enable algal bloom to develop catastrophically (Hughes, 1994). Populations of the large varieties of whales, those that have been most heavily exploited, have been cut to a tiny fraction of their former sizes, and the hunting, especially by the Russians and the Japanese, still goes on, although since the 1980s most nations have banned whaling.

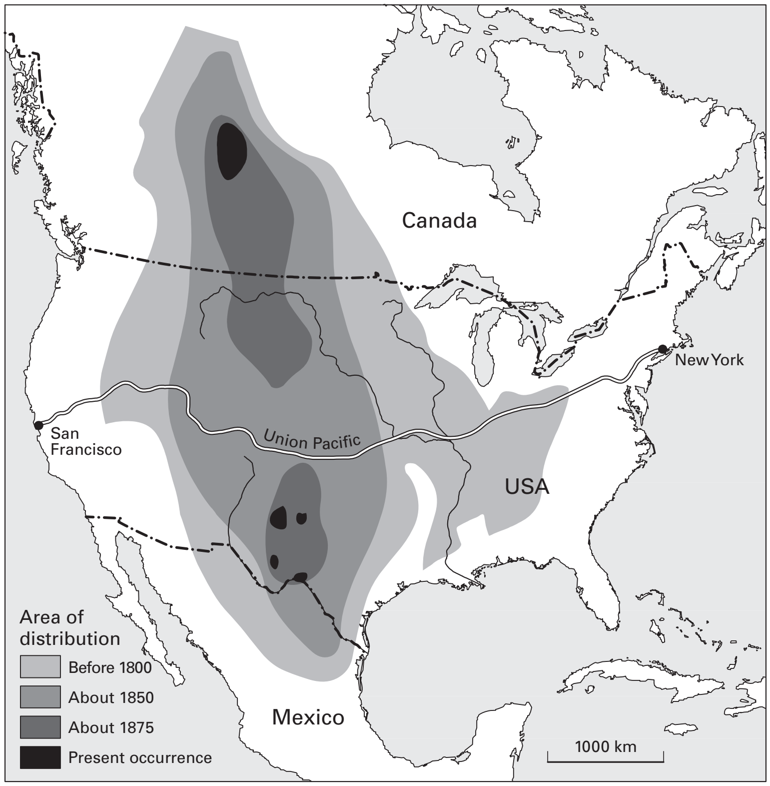

Figure 3.15 The former and present distribution of the bison in North America (after Ziswiler, in Illies, 1974, figure 3.1).

It is extremely difficult to estimate whale stocks before whaling began and therefore to quantify the magnitude of hunting effects that have taken place. However, genetic techniques have recently been used to establish pre-whaling stocks (Roman and Palumbi, 2003). These techniques have indicated that previous estimates of natural stocking levels were too low and that current populations are a fraction of past numbers. Pre-whaling populations in the North Atlantic of humpback, fin, and minke whales were perhaps 865,000 in total, whereas current populations are 215,000. With bans on whaling that now exist, a number of large whale species have shown signs of recovery, although the status of some baleen whale populations continues to cause concern. In addition even if commercial whaling was banned in perpetuity, whales would face other threats of mankind's making, including acoustic disturbance from seismic exploration, sonar, and motor-vessel traffic.

The introduction of a new animal species can cause the decline of another, whether by predation, competition, or by hybridization. This last mechanism has been found to be a major problem with fish in California, where many species have been introduced by humans. Hybridization results when fish are transferred from one basin to a neighboring basin, since closely related species of the type likely to hybridize usually exist in adjacent basins. One species can eliminate another closely related to it through genetic swamping (Moyle, 1976).

Animal extinctions in prehistoric times

Some workers, notably Martin (1967, 1974), believe that the human role in animal extinctions goes back to the Stone Age and to the Late Pleistocene. They believe that extinction closely follows the chronology of the spread of prehistoric civilization and the development of big-game hunting. They would also maintain that there are no known continents or islands in which accelerated extinction definitely pre-dates the arrival of human settlements. An alternative interpretation, however, is that the Late Pleistocene extinctions of big mammals were caused by the rapid and substantial changes of climate at the termination of the last glacial (Martin and Wright, 1967; Martin and Klein, 1984). Martin (1982) argues that the global pattern of extinctions of the large land mammals follows the footsteps of Paleolithic settlements. He suggests that Africa and parts of southern Asia were affected first, with substantial losses at the end of the Acheulean, around 200,000 years ago. Europe and northern Asia were affected between 20,000 and 10,000 years ago, while North and South America were stripped of large herbivores between 12,000 and 10,000 years ago. Megafaunal extinctions in Australia may have occurred around 41,000 years ago, shortly after human arrivals (Roberts et al., 2001). Extinctions continued into the Holocene on oceanic islands and in the Galapagos Islands, for example, virtually all extinctions took place after the first human contact in AD 1535 (Steadman et al., 1991). Likewise the complete deforestation of Easter Island in the Pacific between 1200 and 800 years BP was an ecological disaster that led to the demise of much of the native flora and fauna and also precipitated the decline of the megalithic civilization that had erected the famous statues on the islands (Flenley et al., 1991). As Burney (1993: 536) has written:

> For millennia after the late-Pleistocene extinctions, these seemingly fragile and ungainly ecosystems apparently thrived throughout the world. This is one of the soundest pieces of evidence against purely climatic explanations for the passing of Pleistocene faunas. In Europe, for instance, the last members of the elephant family survived climatic warming not on the vast Eurasian land mass, but on small islands in the Mediterranean.

The dates of the major episodes of Pleistocene extinction are crucial to the discussion. Martin (1967: 111–15) writes:

> Radiocarbon dates, pollen profiles associated with extinct animal remains, and new stratigraphic and archaeological evidence show that, depending on the region involved, late-Pleistocene extinction occurred either after, during or somewhat before worldwide climatic cooling of the last maximum . . . of glaciation . . . Outside continental Africa and South East Asia, massive extinction is unknown before the earliest known arrival of prehistoric man. In the case of Africa, massive extinction coincides with the final development of Acheulean hunting cultures which are widespread throughout the continent . . . The thought that prehistoric hunters ten to fifteen thousand years ago (and in Africa over forty thousand years ago) exterminated far more large animals than has modern man with modern weapons and advanced technology is certainly provocative and perhaps even deeply disturbing.

The nature of the human impact on animal extinctions can conveniently be classified into three types (Marshall, 1984): the 'blitzkrieg effect', which involves rapid deployment of human populations with big-game hunting technology so that there is very rapid demise of animal populations; the 'innovation effect', whereby long-established human population groups adopt new hunting technologies and erase fauna that have already been stressed by climatic changes; and the 'attrition effect', whereby extinction takes place relatively slowly after a long history of human activity because of loss of habitat and competition for resources.

The arguments that have been used in favor of an anthropogenic interpretation can be summarized as follows. First, massive extinction in North America seems to coincide in time with the arrival of humans in sufficient quantity and with sufficient technological skill in making suitable artifacts (the bifacial Clovis blades) to be able to kill large numbers of animals (Krantz, 1970). Second, in Europe the efficiency of Upper Paleolithic hunters is attested by such sites as Solutré in France, where a late Perigordian level is estimated to contain the remains of over 100,000 horses. Third, many beasts unfamiliar with people are remarkably tame and stupid in their presence, and it would have taken them a considerable time to learn to flee or seek concealment at the sight or scent of human life. Fourth, humans, in addition to hunting animals to death, may also have competed with them for particular food or water supplies or may have introduced predators, such as the dingo in Australia, which then competed with native fauna (Johnson and Wroe, 2003). Fifth, Coe (1981, 1982) has suggested that the supposed preferential extinction of the larger mammals could also lend support to the role of human actions. He argues that while large body size has certain definite advantages, especially in terms of avoiding predation and being able to cover vast areas of savanna in search of food, large body size also means that these herbivores are required to feed almost continuously to sustain a large body mass. Furthermore, as the size and generation time of a mammal increases, the rate at which they turn over their biomass decreases (Figure 3.16).

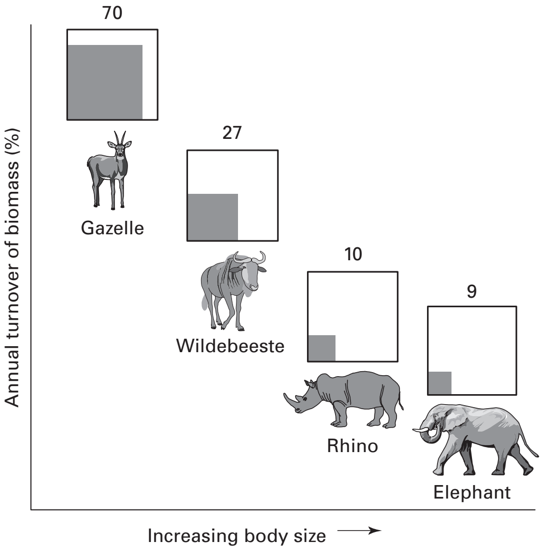

Figure 3.16 Decreasing rate of population biomass turnover with increasing body size in warm- and cold-blooded vertebrates, with some mammal examples illustrated (from Coe, 1982).

Hence a population of Thompson's gazelle will turn over up to 70% of their biomass each year, a wildebeest over 27%, but a rhino only 10% and the elephant just 9%. The significance of this is that, since large mammals can only turn over a small percentage of their population biomass each year, the rate of slaughter that such a population can sustain in the face of even a primitive hunter is very low indeed.

Certain objections have been leveled against the climatic change model and these tend to support the anthropogenic model. It has been suggested, for instance, that changes in climatic zones are generally sufficiently gradual for beasts to be able to follow the shifting vegetation and climatic zones of their choice. Similar environments are available in North America today as were present, in different locations and in different proportions, during Late Pleistocene times. Second, it can be argued that the climatic changes associated with the multiple glaciations, interglacials, pluvials, and interpluvials do not seem to have caused the same striking degree of elimination as those in the Late Pleistocene. A third difficulty with the climatic-cause theory is that animals such as the mammoth occupied a broad range of habitats from arctic to tropical latitudes, so it is unlikely all would perish as a result of a climatic change (Martin, 1982).

This is not to say, however, that the climatic hypothesis is without foundation or support. The migration of animals in response to rapid climatic change could be halted by geographic barriers such as high mountain ranges or seas. The relatively rich state of the African big mammalian fauna is due, according to this point of view, to the fact that the African biota is not, or was not, greatly restricted by an insuperable geographical barrier. Another way in which climatic change could cause extinction is through its influence on disease transmission. It has been suggested that during glacials animals would be split into discrete groups cut off by ice sheets but that, as the ice melted (before 11,000 years BP in many areas), contacts between groups would once again be made enabling diseases to which immunity might have been lost during isolation to spread rapidly. Large mammals, because of their low reproduction rates, would recover their numbers only slowly, and it was large mammals (according to Martin) that were the main sufferers in the Late Pleistocene extinctions.

The detailed dating of the European megafauna's demise lends further credence to the climatic model (Reed, 1970). The Eurasiatic **boreal** mammals, such as mammoth, woolly rhinoceros, musk ox, and steppe bison, were associated with and adapted to the cold steppe, which was the dominant environment in northern Europe during the glacial phases of the last glaciation. Each of these forms, especially the mammoth and the steppe bison, had been hunted by humans for tens of thousands of years, yet managed to survive through the last glacial. They appear to have disappeared, according to Reed, within the space of a few hundred years when warm conditions associated with the Alleröd Interstadial led to the restriction and near disappearance of their habitat.

Grayson (1977) has added to the doubts expressed about the anthropogenic overkill hypothesis. He suggests that the overkill theory, because it states that the end of the North American Pleistocene was marked by extraordinary high rates of extinction of mammalian genera, requires terminal Pleistocene mammalian generic extinctions to have been relatively greater than generic extinctions within other classes of vertebrates at this time. When he examined the extinction of birds he found that an almost exactly comparable proportion became extinct at the end of the Pleistocene as one finds for the megafauna. Moreover, as the radiocarbon dates for early societies in countries such as Australia are pushed back, it becomes increasingly clear that humans and several species of megafauna were living together for quite long periods, thereby undermining the notion of rapid overkill (Gillespie et al., 1978).

Further arguments can be marshalled against the view that humans as predators played a critical role in the Late Pleistocene extinctions in North America (Butzer, 1972: 509–10). There are, for example, relatively few Paleo-Indian sites over an immense area, and the majority of these have a very limited cultural inventory. In addition there is no clear evidence that Paleo-Indian subsistence was necessarily based, in the main part, on big-game hunting; if it was, only two genera were hunted intensively: mammoth and bison. A final point that militates against the argument that humans were primarily responsible for the waves of extinction is the survival of many big-game species well into the nineteenth century, despite a much larger and more efficient Indian population.

Thus the human role in the great Late Pleistocene extinction is still a matter of debate. The problem is complicated because certain major cultural changes in human societies may have occurred in response to climatic change. The cultural changes may have assisted in the extinction process, and increasing numbers of technologically competent humans may have delivered the final coup de grace to isolated remnants already doomed by rapid post-glacial environmental changes (Guilday, 1967). In this context it is worth noting that Haynes (1991) has suggested that at around 11,000 years ago conditions were dry in the interior of the USA and that Clovis hunters may as a result have found large game animals easier prey when concentrated around waterholes and under stress.

Actual extinction may have occurred after or concurrently with a dwarfing in the size of animals, and this too is a subject of controversy (Guthrie, 2003). On the one hand, there are those who believe that the dwarfing could result from a reduction in food availability brought about by climatic deterioration. On the other, it can be maintained that this phenomenon derives from the fact that small animals, being more adept at hiding and being a less attractive target for a hunter, are more likely to survive human predators, so that a genetic selection towards reduced body size takes place (Marshall, 1984).

Although the debate about the cause of this extinction spasm has now persisted for a long time, there are still great uncertainties. This is particularly true with regard to the chronologies of extinction and of human colonization (Brook and Bowman, 2002). This is particularly so in the context of North America, as noted by Grayson (1988). It is probable that the Late Pleistocene extinctions themselves had major ecological consequences. As Birks (1986: 49) has put it:

> The ecological effects of rapid extinction of over 75% of the New World's large herbivores . . . must have been profound, for example on seed dispersal, browsing, grazing, trampling and tree regeneration . . . large grazers and browsers such as bison, mammoth and woolly rhinoceros may have been important in delaying or even inhibiting tree growth.

Modern-day extinctions

As the size of human populations has increased and technology has developed, humans have been responsible for the extinction of many species of animals and a reduction in biodiversity – 'the only truly irreversible global environmental change the Earth faces today' (Dirzo and Raven, 2003). Indeed, it has often been maintained that there has been a close correlation between the curve of population growth since the mid-seventeenth century and the curve of the number of species that have become extinct (Figure 3.17a, b). However, although it is likely that European expansion overseas during that time has led to many extinctions, the dramatic increase in the rate of extinctions over the past few centuries that is shown in the figure may in part be a consequence of a dramatic increase in the documentation of natural phenomena.

A more recent attempt to look at the historical trends in extinction rates (Figure 3.17c) for 20-year intervals from the year 1600 shows a rather different pattern, with a decline in rate for 1960–1990. This may partly be because of a time lag in the recording of the most recent extinction events, but it may also be the result of successful conservation efforts and the spread of the areal extent of protected areas. What is clear, however, is just what a large proportion of total extinctions have been recorded from islands.

When considering modern-day extinctions the role of human agency is much less controversial. Nonetheless,

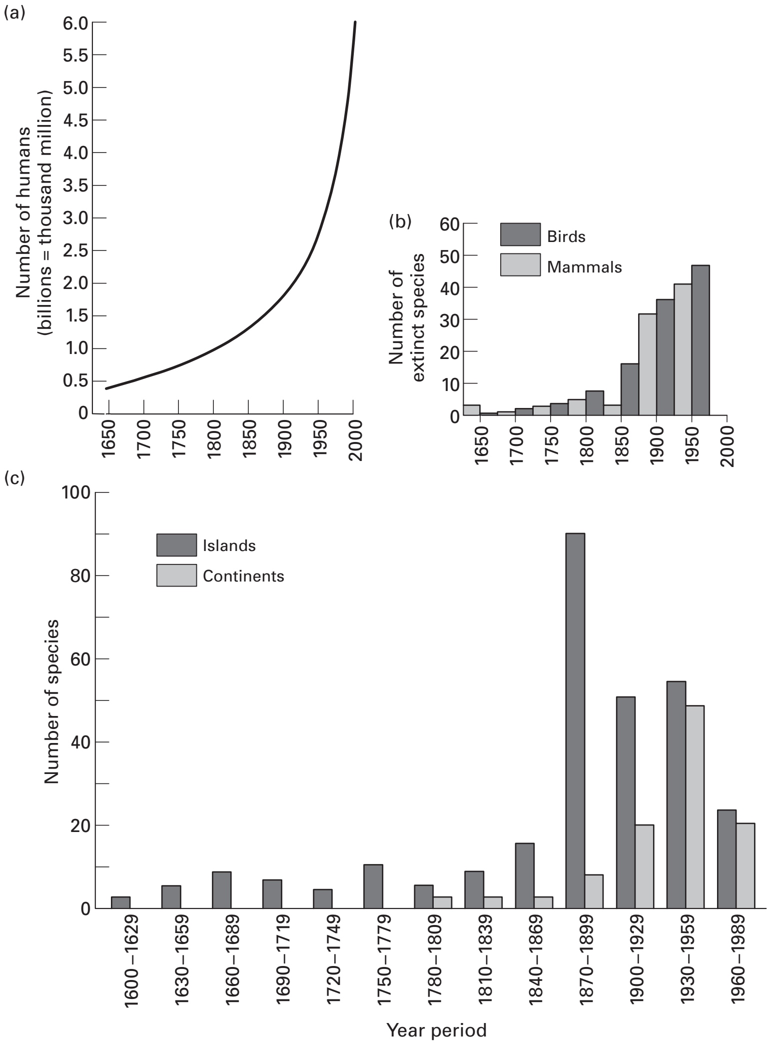

Figure 3.17 Time series of animal extinctions since the seventeenth century, in relation to human population increase (a). Figure (b) shows an early attempt to trace the number of extinctions in birds and mammals (after Ziswiler in National Academy of Sciences, 1972, figure 3.2), while figure (c) is a more recent attempt and displays a decreasing rate of animal extinctions in recent decades (after World Conservation Monitoring Centre, 1992, figure 16.5).

some modern extinctions of species are natural. Extinction is a biological reality: it is part of the process of evolution. In any period, including the present, there are naturally doomed species, which are bound to disappear, either through overspecialization or an incapacity to adapt themselves to climatic change and the competition of others, or because of natural cataclysms such as earthquakes, volcanic eruptions, and floods. Fisher et al. (1969) believe that probably one-quarter of the species of birds and mammals that have become extinct since 1600 may have died out naturally. In spite of this, however, the rate of animal extinctions brought about by humans in the past 400 years is of a very high order when compared with the norm of geologic time. In 1600 there were approximately 4226 living species of mammals: since then 36 (0.85%) have become extinct; and at least 120 of them (2.84%) are presently believed to be in some (or great) danger of extinction. A similar picture applies to birds. In 1600 there were about 8684 living species; since then 94 (1.09%) have become extinct, and at least 187 of them (2.16%) are presently, or have very lately been, in danger of extinction (Fisher et al., 1969).

Some beasts appear to be more prone to extinction than others, and a distinction is now often drawn between *r*-selected species and *k*-selected species. These are two ends of a spectrum. The former have a high rate of increase, short gestation periods, quick maturation, and the advantage that they have the ability either to react quickly to new environmental opportunities or to make use of transient habitats (such as seasonal ponds). The life duration of individuals tends to be short,

Table 3.6 Characteristics of species affecting survival

Endangered	*Safe*
Large size	Small size
Predator	Grazer, scavenger, insectivore
Narrow habitat tolerance	Wide habitat tolerance
Valuable fur, oil, hide, etc.	Not a source of natural products
Restricted distribution	Broad distribution
Lives largely in international waters	
Migrates across international boundaries	Lives largely in one country
Reproduction in one or two vast aggregates	Reproduction by solitary pairs or in many small aggregates
Long gestation period	Short gestation period
Small litters	Big litters and quick maturation
Behavioral idiosyncrasies that are nonadaptive today	Adaptive
Intolerance to the presence of humans	Tolerance of humans
Dangerous to humans, livestock, etc.	Perceived as harmless

populations tend to be unstable, and the species may overexploit their environment to their eventual detriment. Many pests come into this category. At the other end of the spectrum the *k*-selection species are those which tend to be endangered or to become extinct. Their prime characteristics are that they are better adapted to physical changes in their environment (such as seasonal fluctuations in temperature and moisture) and live in a relatively stable environment (Miller and Botkin, 1974). These species tend to have much greater longevity, longer generation times, fewer offspring, but a higher probability of survival of young and adults. They have traded a high rate of increase and the ability to exploit transient environments for the ability to maintain more stable populations with low rates of increase, but correspondingly low rates of mortality and a closer adjustment to the long-term capacity of the environment to support their population.

Table 3.6, which is modified after Ehrenfield (1972), attempts to bring together some of the characteristics of species that affect their survival in the human world. This is also a theme discussed in Jeffries (1997).

There are at least nine ecological or life history traits that have been proposed as factors which determine the sensitivity of an animal species to a reduction and fragmentation in habitat (World Conservation Monitoring Centre, 1992: 193):

> *Rarity*
> Several studies have found that the abundance of a species prior to habitat fragmentation is a significant predictor of extinction . . . This is only to be expected, since fewer individuals of a rare species than a common species are likely to occur in habitat fragments, and the mechanisms of extinction mean that small populations are inherently more likely to become extinct than large.
>
> *Dispersal ability*
> If animals are capable of migrating between fragments or between 'mainland' areas and fragments, the effects of small population size may be partly or even greatly mitigated by the arrival of 'rescuers'. Species that are good dispersers may therefore be less prone to extinction in fragmented habitats than poor dispersers.
>
> *Degree of specialization*
> Ecological specialists often exploit resources which are patchily distributed in space and time, and therefore tend to be rare. Specialists may also be vulnerable to successional changes in fragments and to the collapse of coevolved mutualisms or food webs.
>
> *Niche location*
> Species adapted to, or able to tolerate, conditions at the interface between different types of habitats may be less affected by fragmentation than others. For example, forest edge species may actually benefit from habitat fragmentation.
>
> *Population variability*
> Species with relatively stable populations are less vulnerable than species with pronounced population fluctuations, since they are less likely to decline below some critical threshold from which recovery becomes unlikely.
>
> *Trophic status*
> Animals occupying high trophic levels usually have small populations: e.g., insectivores are far fewer in number than their insect prey and, as noted above, rarer species are more vulnerable to extinction.
>
> *Adult survival rate*
> Species with naturally low adult survival rates may be more likely to become extinct.
>
> *Longevity*
> Long-lived animals are less vulnerable to extinction than short-lived.
>
> *Intrinsic rate of population increase*
> Populations which can expand rapidly are more likely to recover after population declines than those which cannot.

Possibly one of the most fundamental ways in which humans are causing extinction is by reducing the area of natural habitat available to a species (Turner, 1996) and by fragmenting it (Fahrig, 2003). Habitat fragmentation divides once continuous, large populations into many smaller ones, which can be more or less isolated. Small population size and strong isolation of populations are associated with various negative consequences, which include susceptibility to natural disasters, genetic drift, and inbreeding (Lienert, 2004). Even wildlife reserves tend to be small 'islands' in an inhospitable sea of artificially modified vegetation or urban sprawl.

We know from many of the classic studies in true island biogeography that the number of species living at a particular location is related to area (see Figure 3.18

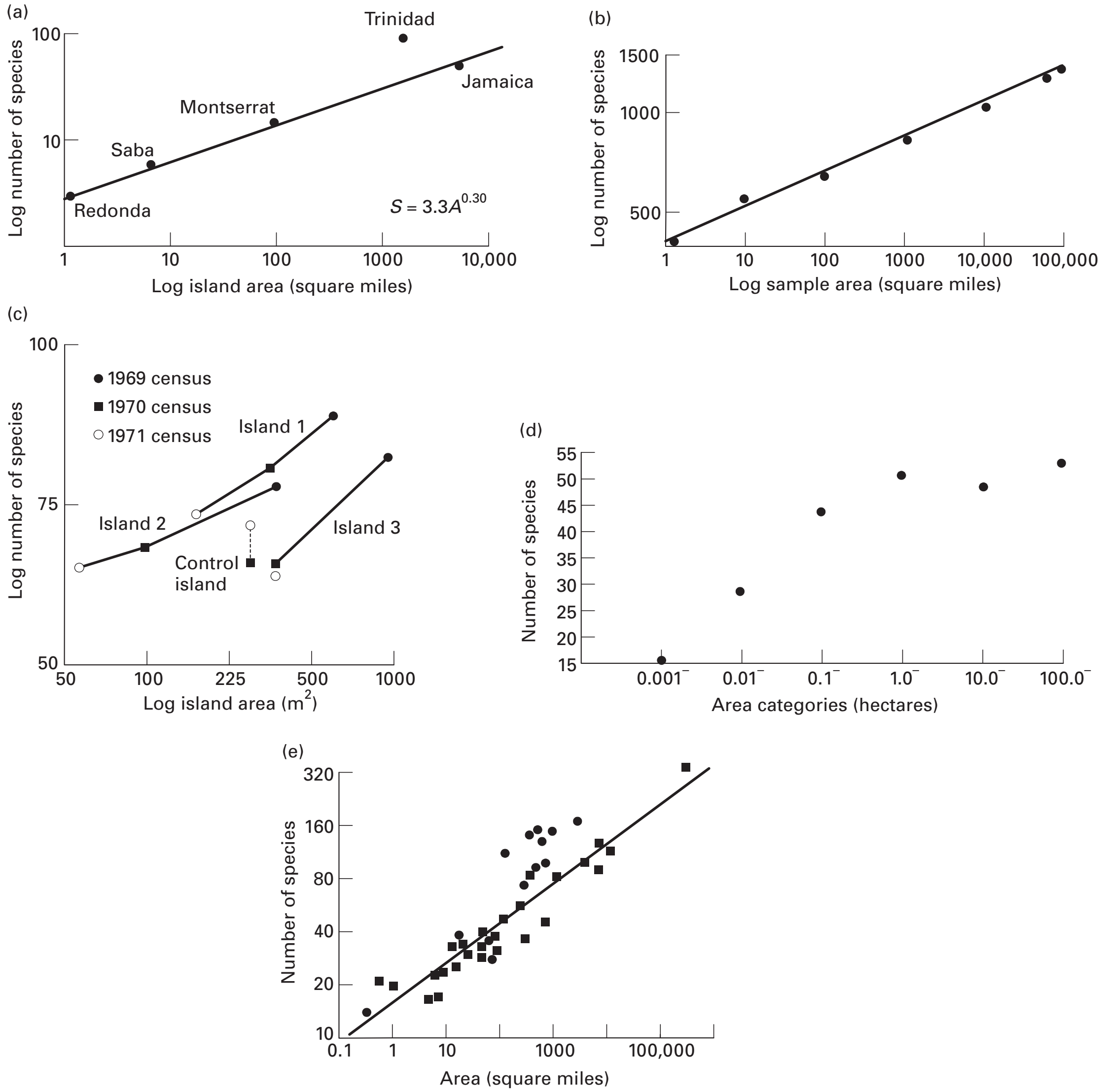

Figure 3.18 Some relationships between the size of 'islands' and numbers of species (after Gorman, 1979, figures 3.1, 3.2, 8.1 and 8.2). (a) The number of amphibian and reptile species living on West Indian islands of various sizes. Trinidad, joined to South America 10,000 years ago, lies well above the species–area curve on other islands. (b) The area–species curve for the number of species of flowering plants found in a sample of area of England. (c) The effect on the number of arthropod species of reducing the size of mangrove islands. Islands 1 and 2 were reduced after both the 1969 and the 1970 census. Island 3 was reduced only after the 1969 census. The control island was not reduced, the changes in species number being attributable to random fluctuation. (d) The number of species of bird living in British woods of various size categories. (e) The number of species of land birds living in the lowland rainforest on small islands in New Guinea, plotted as a function of island area. The squares represent islands which have not had a land connection to New Guinea and whose avifaunas are at equilibrium. The regression line is fitted through these points. The circles represent former land-bridge islands connected to New Guinea some 10,000 years ago. Note that the large ones have more species than one would expect for their size.

for some examples); islands support fewer species than do similar areas of mainland, and small islands have fewer species than do large ones. Thus it may well follow that if humans destroy the greater part of a vast belt of natural forest, leaving just a small reserve, initially it will be 'supersaturated' with species, containing more than is appropriate to its area when at equilibrium (Gorman, 1979). Since the population sizes of the species living in the forest will now be greatly reduced, the extinction rate will increase and the number of species will decline towards equilibrium. For this reason it may be a sound principle to make reserves as large as possible; a larger reserve will support more species at equilibrium by allowing the existence of larger populations with lower extinction rates. Several small reserves will plainly be better than no reserves at all, but they will tend to hold fewer species at equilibrium than will a single reserve of the same area (Figure 3.19). If it is necessary to have several small reserves, they should be placed as close to each other as possible so that each may act as a source area for the others. Connectivity of reserves is an important issue, and if it can be achieved their equilibrial number of species will be raised due to increased immigration rates.

There are situations when small reserves may have advantages over a single large reserve: they will be less prone to total decimation by some natural catastrophe such as fire; they may allow the preservation of a range of rare and scattered habitats; and they may allow the survival of a group of competitors, one of which would exclude the others from a single reserve.

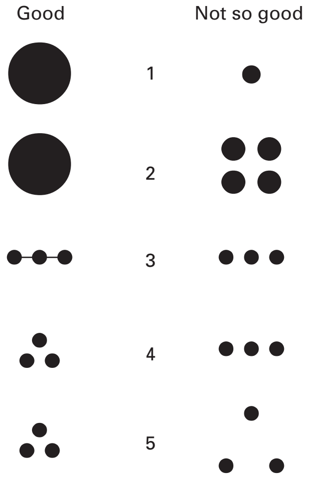

Figure 3.19 A set of general design rules for nature reserves based on theories of island biogeography. The designs on the left are preferable to those on the right because they should enjoy lower rates of species extinction. (1) A large reserve will hold larger populations with lower probabilities of going extinct than a small reserve. (2) A single reserve is preferable to a series of smaller reserves of equal total area, since these will support only small populations with relatively high probabilities of going extinct. (3–5) If reserves must be fragmented, then they should be connected by corridors of similar vegetation or be placed equidistant and as near to each other as possible. In this way immigration rates between the fragments will be increased, thereby maximizing the chances of extinct populations being replaced from elsewhere in the reserve complex (after Gorman, 1979, figure 8.4).

Reduction in area leads to reduction in numbers, and this in turn can lead to genetic impoverishment through inbreeding (Frankel, 1984). The effect on reproductive performance appears to be particularly marked. Inbreeding degeneration is, however, not the only effect of small population size for, in the longer term, the depletion of genetic variance is more serious since it reduces the capacity for adaptive change. Space is therefore an important consideration, especially for those animals that require large expanses of territory. For example, the population density of the wolf is about one adult per 20 km^2, and it has been calculated that for a viable population to exist one might need 600 individuals ranging over an area of 12,000 km^2. The significance of this is apparent when one realizes that most nature reserves are small: 93% of the world's national parks and reserves have an area less than 5000 km^2, and 78% less than 1000 km^2.

Equally, range loss, the shrinking of the geographical area in which a given species is found, often marks the start of a downward spiral towards extinction. Such a contraction in range may result from habitat loss or from such processes as hunting and capture. Particular concern has been expressed in this context about the pressures on primates, notably in Southeast Asia. Of 44 species, 33 have lost at least half their natural range in the region. In two cases, those of the Javan leaf monkey and the Javan and gray gibbons, the loss of range is no less than 96%. Recent figures produced by the International Union for the Conservation of Nature and the United Nations Environment Program for wildlife habitat loss show the severity of the problem

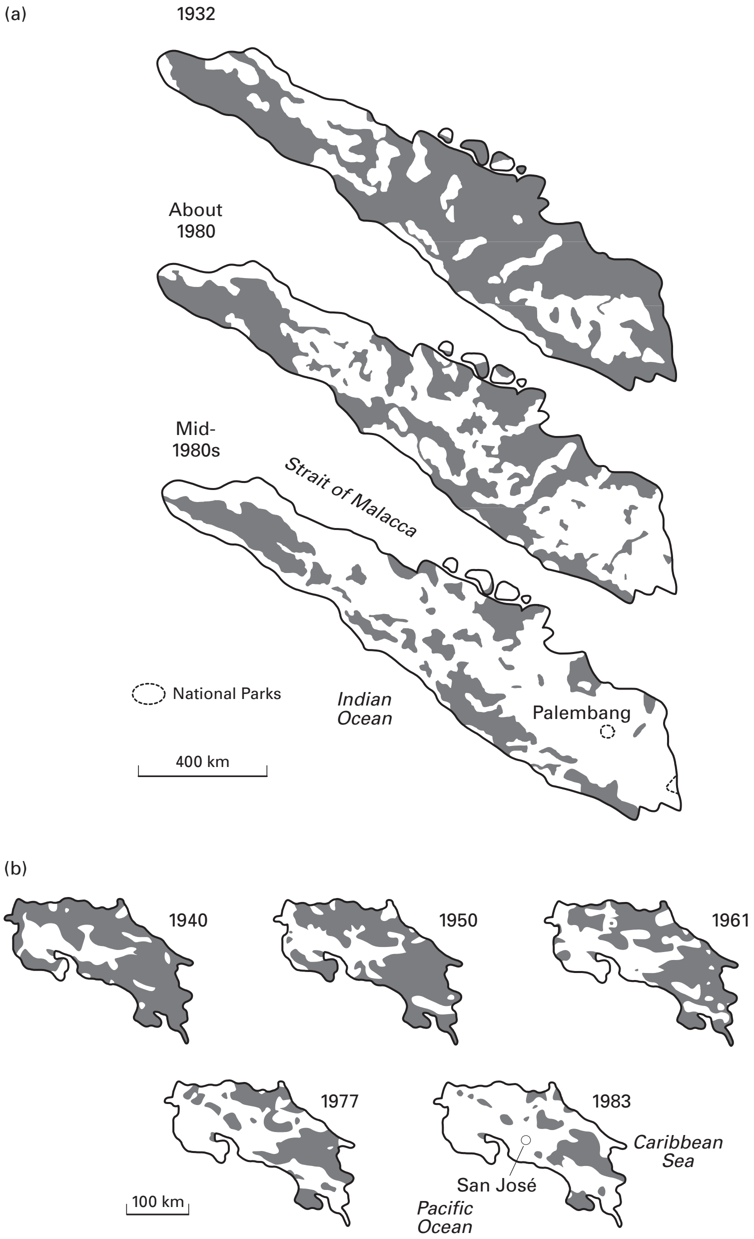

Figure 3.20 Progressive habitat fragmentation in the rainforest environments of (a) Sumatra and (b) Costa Rica (modified after Whitten et al., 1987 and Terborgh, 1992).

(see World Resources Institute, 1988, tables 6.4 and 6.5). In the Indomalayan countries 68% of the original wildlife habitat has been lost, and the comparable figure for tropical Africa is 65%. In these regions, only Brunei and Zambia have lost less than 30% of their original habitat, while at the other end of the spectrum Bangladesh, the most densely populated large country in the world, has suffered a loss of 94%. Figure 3.20 shows the fragmentation and reduction in area of rainforest within two areas: Sumatra and Costa Rica.

Although habitat change and destruction is clearly a major cause of extinction in the modern era, a remarkably important cause is the introduction of competitive species (Figure 3.21). When new species are deliberately or accidentally introduced to an area, they can cause the extermination of local fauna by preying on them or out-competing them for food and space. As we have seen elsewhere island species have proved to be especially vulnerable. The World Conservation Monitoring Centre, in its analysis of the known causes

Figure 3.21 The Fynbos of the Cape Region of South Africa is a biodiversity hot spot that has a great diversity of flora and fauna. It is a habitat that is under a number of threats, including the invasion of competitive species from Australia, which smother the native heathland.

of animal extinctions since AD 1600, believed that 39% were caused by species introduction, 36% by habitat destruction, 23% by hunting, and 2% for other reasons (World Resources Institute, 1996: 149).

There are certainly some particularly important environments in terms of their species diversity (Myers, 1990) and such biodiversity 'hot spots' (Figure 3.22) need to be made priorities for conservation. They include coral reefs, tropical forests (which support well over half the planet's species on only about 6% of its land area), and some of the Mediterranean climate ecosystems (including the extraordinarily diverse Fynbos shrublands of the Cape region of South Africa). Some environments are crucial because of their high levels of species diversity or endemic species; others are crucial because their loss would have consequences elsewhere. This applies, for example, to wetlands, which provide habitats for migratory birds and produce the nutrients for many fisheries. Myers et al. (2000) has argued that as many as 44% of all species of vascular plants and 35% of all species in four groups of vertebrate animals are confined to just 25 hot spots that comprise a mere 1.4% of Earth's land surface. These are major locations for conservation.

Finally, future climate change could act as a major cause of extinctions in the coming decades and could be a major threat to biodiversity (Thomas et al., 2004).

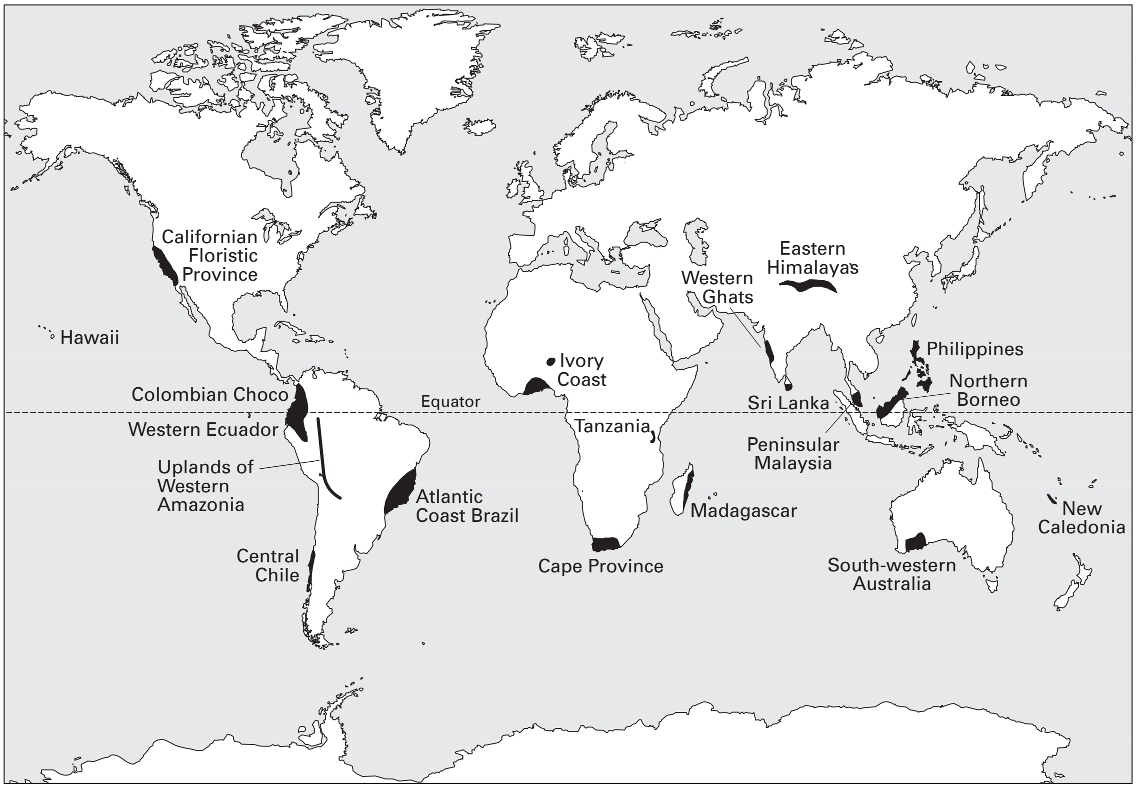

Figure 3.22 Forest and heathland hot-spot areas. Hot spots are habitats with many species found nowhere else and in greatest danger of extinction from human activity (after Wilson, 1992: 262–3)

As we will see in Chapters 8 to 13, many habitats will change markedly, and as a result many nature reserves will be in the wrong place for the species they are meant to protect. For instance, high altitude habitats at the tops of mountains may simply disappear.

Points for review

What do you understand by plant and animal domestication?

What are the ecological effects of invasive animals?

What are the main factors that lead to declines in animal populations?

Why did some animals become extinct in prehistoric times?

Guide to reading

Clutton-Brock, J., 1987, *A natural history of domesticated mammals*. London: British Museum and Cambridge: Cambridge University Press. A global survey of the domestication of a wide range of animals from asses to zebu cattle.

Drake, J. A., et al. (eds), 1989, *Biological invasions. A global perspective*. Chichester: Wiley. An edited paper of essays that considers both animal and plant invaders.

Martin, P. S. and Klein, R. G., 1984, *Pleistocene extinctions*. Tucson: University of Arizona Press. An enormous survey of whether or not late Pleistocene extinctions were caused by humans.

Wilson, E. O., 1992, *The diversity of life*. Harvard: Belknap Press. A beautifully written and highly readable discussion of biodiversity.