

When you have read this chapter you will have been introduced to:

- evolution
- · evolutionary strategies and game theory
- adaptation
- · dispersal mechanisms
- species and habitats
- biodiversity
- fisheries
- forests
- agriculture
- human populations and demographic change
- genetic engineering

46 Evolution

Evolution is the formation of new species from pre-existing species. That is all the word means to biologists and it implies nothing with regard to the steps that might be involved. The word is often linked to the name of Darwin, giving the impression that in some sense he invented the concept. This is quite untrue. The evolution of species from pre-existing species was widely (although not universally) accepted by the time Darwin began to think about it seriously and today it is not in the least controversial. The evolution of species is a fact, well documented and observed.

Darwin contributed to the concept the proposal of a mechanism by which the evolutionary process may occur. He called it 'natural selection', and after his death its merging with the growing body of knowledge about genetics led some people to rename 'Darwinism' 'neo-Darwinism' or 'the modern synthesis'. Nevertheless, it remains fundamentally the explanation Darwin proposed.

Today the great majority of biologists accept Darwinism as a valid explanation for evolution in general. There is argument about details and particular instances, but these tend to strengthen the Darwinian proposition rather than weaken it. When scientists talk of the 'theory of evolution', it is the Darwinian theory, of evolution by means of natural selection, to which they refer and they give 'theory' its scientific meaning of an explanation for observed phenomena. Never do they seek to imply that evolution itself is no more than a vague, albeit attractive, idea. To misuse the word 'theory' in this way, and to conflate the Darwinian theory with the observed fact of evolution, betokens ignorance or intellectual dishonesty.

Evolution proceeds from natural selection and at the centre of this concept lies the idea of 'adaptedness'. This is the degree to which a species is suited to the conditions under which it lives. Those conditions vary from place to place and time to time, and the degree of adaptedness varies from one individual to another. These variations provide the 'raw material' on which evolution

operates and its operation leads to 'speciation', which is the dividing of one species into two that in principle (but not always in fact) are unable to interbreed.

Consider the plight of the Red Queen. She explained to Alice that: 'Now, *here*, you see, it takes all the running *you* can do, to keep in the same place. If you want to get somewhere else, you must run at least twice as fast as that!' Species adapt to the environmental conditions to which they are exposed, but those conditions include other species with which they interact. Among a prey species, for example, those individuals that run fastest may be more likely to escape capture. They survive to breed and so the species as a whole comes to comprise animals that run faster than did their ancestors. Their predators, however, are also likely to evolve means of countering this development. Perhaps they, too, will come to run faster or perhaps they will acquire new hunting strategies. Thus natural selection can place species in a situation closely resembling that of the Red Queen in *Through the Looking Glass*, running, or adapting, as fast as they can merely to remain in the same place. In 1973, L.Van Valen called this the Red Queen effect and that is the name by which it is now known (COCKBURN, 1991, p. 125).

Environments are often exceedingly complex, however, and the image of large predators hunting grazing herbivores across the plains of Africa is not typical. It is better to picture an environment, and the relationships producing natural selection within it, as something at once smaller and richer in detail, perhaps in the way Charles Darwin described it:

It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us (DARWIN, 1859).

This generates a quite different picture and suggests quite different strategies. Although they have not been investigated so thoroughly as the Red Queen effect, the Tangled Bank hypothe-ses, proposed by G.Bell in 1982, suggest that while a species may be well adapted to its immediate surroundings, its offspring may not inherit that advantage. Offspring may increase their chances of survival, therefore, if they disperse randomly into neighbouring habitats where they will encounter slightly different conditions that will favour at least some of them, because of the natural variation between one individual and another. If true, this implies that sexually reproducing organisms are better equipped to enter and exploit new habitats than those which reproduce asexually and therefore produce offspring that are genetically identical to one another and to their parent (i.e. that are clones). It also implies that competition among siblings is reduced in sexually reproducing species.

Evolution is believed to proceed essentially in the manner proposed by Darwin (see box).

Natural selection

Darwin proposed a theory that can be expressed very simply. It proceeds by the operation of natural selection on the variation within populations.

- 1 Within any population of a species, individuals are not identical in every respect.
- 2 Populations generally produce more offspring than are required to replace their parents.

- 3 On average, population numbers remain stable, and clearly no population can increase in number indefinitely.
- 4 Competition for breeding opportunities, food, and other resources must therefore occur among offspring, only some of which survive long enough to breed.
- 5 The survivors are those best adapted to the environment, in other words the fittest.

It was the English philosopher Herbert Spencer (1820–1903) who described Darwin's theory as the 'survival of the fittest', a phrase Darwin disliked, although he used it more or less as a synonym for natural selection in later editions of *On the Origin of Species by Means of Natural Selection*, and Alfred Russel Wallace (1823–1913), the co-discoverer of the theory of evolution by natural selection, used it unreservedly (OLDROYD, 1980, pp. 107 and 117). Critics, however, pointed out an apparent weakness. 'Survival' means remaining alive and, it seems, the fittest can be identified by the fact that they survive, so perhaps 'survival of the fittest' can be rephrased as 'survival of the survivors', which is tautological and leads to a circular argument: we identify the fittest (i.e. the survivors) by the fact of their survival (RIDLEY, 1985, pp. 29–30).

In the form in which he presented it, Darwin's theory does, indeed, present difficulties. He believed, for example, that the characteristics of parents are blended in their offspring (a discredited theory called 'blending inheritance') and that, at least to a minor extent, in adapting to environmental pressures, individuals may develop physiologically or behaviourally in ways that are inherited by their offspring (the 'inheritance of acquired characters', another discredited theory). Difficulties there were, but the theory was not tautological.

It avoids tautology by invoking the concept of selection within a changing environment. Consider the well-known case of the development by insects of resistance to insecticides. Within the initial insect population, some individuals will be especially susceptible to a particular insecticide. Most will be susceptible to it, but at a higher dose. There will be just a few, however, that can tolerate the highest dose applied. After one application, all the most susceptible and most of the moder-ately susceptible insects will die, but the tolerant ones will survive. After several applications, the majority of insects will tolerate the insecticide and the population as a whole will have become resistant to it. Selection, in this case not really natural, of course, because the insecticide is applied by humans, drives adaptation, and also explains it.

This kind of phenomenon was demonstrated very dramatically by H.B.D.Kettlewell in 1973 (FORD, 1981, pp. 88–92) (see box) in the case of the peppered moth, although no speciation occurred because the morphs were not isolated from one another and continued to interbreed. It is a precondition for speciation that, for whatever reason, two populations of the same species cease to interbreed. When this happens each can evolve in its own way and that is how one species becomes two.

The peppered moth

The peppered moth (*Biston betularia*) rests on tree trunks and wooden fences and is hunted by birds, which seek their prey visually. The moth is polymorphic. That is to say, it exists in several forms. Some are pale, others progressively darker. In 1848, the first dark moth (*carbonaria*) was reported near Manchester; by 1895, 98 per cent of the moths were of the *carbonaria* morph. Between 1848 and 1895, soot from factory chimneys had blackened trees and fences around Manchester. H.B.D.Kettlewell bred pale and dark moths and released them, watching with binoculars to see how they fared. When pale moths alighted on clean, lichen-covered trees they were almost invisible, but when they alighted on blackened trees they were clearly seen by their predators. As air pollution decreased, the trees and fences became cleaner, making the *carbonaria* moths more visible, and the pale morphs became commoner, intermediate morphs doing well in the areas through which the amount of pollution was decreasing.

Should the environmental pressure causing selection continue for long enough, members of the adapted population may become sufficiently different from those of the ancestral population and neighbouring populations not subjected to the pressure as to be unable to interbreed with them. At this point, the reproductively isolated population is classified as a new species. It follows, therefore, that natural selection acting on natural variation also explains the evolution of species.

In these cases, natural selection drives variation in a particular direction. This is called 'directional selection' and it is one of the three ways natural selection can influence evolution. Most individuals in a polymorphic population will be 'average', the numbers of variants decreasing as their variation becomes increasingly extreme. Presented graphically, this produces the bell-shaped curve shown as the solid line in the first graph in Figure 5.1. If selection favours one of the variants, after several generations these will become the new 'average' and the population will have changed in the direction of that variant, shown by the broken curve.

Suppose that then the environment remains constant. Selection now favours the average individual at the expense of variants. The bell-shaped curve remains where it is, but becomes taller and narrower (the broken line) as the extreme variants disappear from the population. This is called 'stabilizing selection' and is illustrated by the second graph in Figure 5.1. By favouring average individuals, this can reduce the number of variant types and, by depleting the evolutionary 'raw material', make speciation less likely.

It is possible, however, for two extreme forms to be selected, as shown by the third graph. Again, the selected variants become the average, but now there are two average types and two bell-shaped curves (broken line). This is 'disruptive selection' and may lead to the isolation of two distinct morphs that eventually evolve into distinct species.

Darwin knew from observation that variation exists among individuals within any population, but he had no explanation for the cause of that variation or for the way variations were inherited. This was a major weakness in his theory, of which he was well aware, and he died without learning that it had been resolved in 1866 by an obscure Austrian monk in a paper published in the *Transactions of the Brünn Natural History Society*. If, as Darwin believed, offspring inherited a blend of their parents' characteristics, variation within populations would gradually even out through random matings, leaving nothing on which natural selection could act. What the paper showed was that offspring do not inherit a blend of characters; that is not how heredity operates.

The monk, Gregor Johann Mendel (1822–84), spent eight years growing peas in the garden at St Thomas Monastery in Brünn (now Brno, in the Czech Republic), his experiments ending when



Figure 5.1 Effects of natural selection

his election as abbot, in 1868, left him too little time to continue them. He discovered that heritable characters are controlled by 'factors' (now called genes) which individuals possess in pairs (now called alleles). When gametes (egg and sperm cells) form, each contains only one version (allele). This is now known as Mendel's first law, or the law of segregation. Mendel's second law, or the law of independent assortment, states that when gametes combine at fertilization, the alleles behave independently, combining randomly with corresponding alleles. This is now known to apply only to genes that are not closely linked on the same chromosome; these tend to remain together.

Mendel worked with tall and short peas. Expressed in modern terms, his peas possessed two tallness alleles. One, call it T, is dominant: any pea inheriting T will be tall. The other, call it t, is recessive.

The consequences of this arrangement are shown in Figure 5.2. If TT is crossed with tt, all offspring will be Tt, and thus tall. If Tt is crossed with another Tt, 75 per cent of the offspring will be Tt and thus tall, and 25 per cent tt and short. Mendel died in obscurity, and it was not until 1900 that his work was rediscovered independently by three botanists studying the past literature in connection with their own work.

Variation within populations results from the mutation in the genes of gametes (the cells which fuse at fertilization and develop to form a new individual) and by the shuffling of genes. DNA (deoxyribonucleic acid) is the substance by which heritable char-acters are transmitted from one generation to the next, and changes in the units of which it is composed, the order in



Figure 5.2 Mendelian inheritance

which they are arranged, or the amount of genetic material (as in polyploidy, where the number of chromosomes increases) alter the effects they produce. Such changes, called mutations, occur randomly from a wide variety of causes. Many mutations cause the death of the cell in which they occur or of the entire organism, but some have no great effect. Eventually these become established within a population, bringing about a gradual change in its genetic composition, called 'genetic drift'. Should the environment change, natural selection acts on mutant organisms.

Natural selection acts upon individual organisms, but evolution occurs at the molecular level; it acts on genes. The genetic constitution of an organism is known as its 'genotype', and its physical characteristics, or the expression of its genotype, are its 'phenotype'.

Genetics combined with evolutionary ecology can explain much about the way organisms adapt to their environments and the links between adaptation and evolution. Not all organisms evolve at the same rate, however. It has been suggested, for example, that birds have evolved very rapidly, with all modern types having appeared during the last 5–10 million years (STOCK, 1995). There is also some evidence that the rate of evolution has slowed in humans (GIBBONS, 1995).

The concept of a species is convenient, but it is no longer so secure as it used to be. Many genes occur in all species, so it makes little sense to think of a 'pig' gene or a 'tomato' gene; there are simply genes. Genetic comparisons within and between species have revealed a great deal of overlap, such that the genetic difference between two individuals of the same species may be greater than that between members of different species. This blurring of what were formerly thought to be sharply defined boundaries between species is highly pertinent to the debate over genetically modified organisms.

Environments are changing constantly and have been doing so since life first appeared on our planet. Were organisms unable to adapt to change, life would have perished long ago, and were natural selection not to lead to the evolution of new species, countless ecological niches would have remained undefined. Environmental change is inevitable and certainly is not to be feared. It is difficult, probably impossible, to imagine any change capable of destroying all life on Earth, short of the eventual and inevitable expansion of the Sun into a red giant.

47 Evolutionary strategies and game theory

Imagine both you and your best friend are criminals. Together, you perform a heinous crime for which you are both arrested some time later. The police place you in separate cells, so you cannot confer, and a detective begins to question you. He admits that although he knows perfectly well that you are both guilty he cannot prove it, so he needs an admission. At this point he makes you an offer and tells you that his colleague is making an identical offer to your friend.

Your offence carries a maximum sentence of 5 years in prison.

If you will swear in court that your friend committed the offence you will go free, but your friend will receive the maximum sentence.

If both of you refuse to implicate the other, you will be convicted of a lesser offence, for which you will go to prison for 2 years.

If both of you implicate the other, both of you will go to prison for 4 years.

What should you do? If you betray your friend you may avoid prison, but what will your friend do? If you remain loyal, but are betrayed, you could go to prison for 5 years. If both of you remain loyal you will still go to prison, but for only 2 years. The trouble is, can you trust your friend?

This conundrum is known as The Prisoner's Dilemma and it is easier to understand if, instead of prison terms, the consequence of each choice is represented as a score, as in a game, and the words 'loyalty' and 'betrayal' are replaced by the more neutral 'cooperate' and 'defect'. In this case we might award scores based on the number of years removed from the sentence, from 0 to 5. The possible options and their scores are shown in Figure 5.3.

Work it out and you may find the result surprising. For each prisoner, or player, the best option is to defect regardless of what the other does. If both cooperate, they each receive 3 points; this is a higher score than they receive if both defect, but carries the risk of a one-sided defection and a zero score. The likelihood, therefore, is that both players will defect (NOWAK *ET AL.*, 1993).



Figure 5.3 The Prisoner's Dilemma

Abstract though it may seem, The Prisoner's Dilemma raises an important question. Since, in any transaction, it pays to cheat, why is it that we feel this is wrong and how is it that in nature we see so many examples of cooperation? Remember that non-humans are not constrained by morality and are impelled by a purely Darwinian urge to maximize their reproductive opportunities.

We are accustomed to thinking of games, like soccer or baseball, that are played once and in which one team or player wins and the other loses. These are known as 'zero-sum' games, because if the winner is given a score of +1 and the loser of -1 the sum of the scores is 0.

Life is not really like that. The games of life, or transactions between organisms, are played many times and usually end only with the deaths of participants. This alters the situation, because the strategy that works well in a one-round, zero-sum game may not succeed over an indeterminate number of rounds. Played many times, The Prisoner's Dilemma becomes what is usually called The Iterated Prisoner's Dilemma.

Some years ago, the British biologist J.Maynard Smith and his colleagues G.R.Price and G.A. Parker borrowed ideas from game theory, a branch of mathematics devised originally to help plan military strategy, and applied them to the evolution of behaviour. Their aim was to discover behavioural strategies that could not be defeated if most members of a population adopted them. Because such a strategy would endure, it was called an 'evolutionarily stable strategy' (ESS). As an apparently simple example, Maynard Smith proposed a population consisting only of hawks and doves. When two individuals meet, hawks always fight as hard as they can, doves never fight; if a dove meets a hawk it runs away and if two doves meet they posture at one another until one retreats, but their contests never come to blows. So, if two hawks meet, one of them is badly wounded or killed; if a hawk and dove meet, the hawk wins but neither is hurt because the dove runs away; if two doves meet neither is hurt, but they waste a good deal of time posturing. There is no way to tell until an encounter whether an individual is a hawk or a dove. The ESS for the population as a whole will be achieved by some ratio of hawks to doves.

If the population consists only of doves, they will prosper, but there is a risk that a hawk will suddenly emerge either by invading or by mutation. A single hawk will have an immense advantage. Hawk numbers will increase until a point is reached at which there is a high probability that hawks will encounter other hawks, rather than doves. This places the hawks at a serious disadvantage. When scores are allotted for the outcomes of encounters, with penalties for injuries and wasting time, it emerges that the population will stabilize at around 42 per cent doves and 58 per cent hawks (DAWKINS, 1978, pp. 75–77).

Natural populations are not composed of individuals that invariably react to encounters in one of two extreme ways, but we need not suppose non-humans capable of thinking through the consequences of their actions to understand how an ESS can evolve. Natural selection acts on behavioural strategies just as it does on physiology, and the behaviour that optimizes reproduction will prevail. Some twenty years ago, Robert Axelrod, a political scientist, challenged computer programmers to devise an undefeatable strategy for The Iterated Prisoner's Dilemma, then played the 63 contest-ing programs against each other repeatedly. The winning strategy, devised by a game theorist, Anatol Rapoport, and called 'Tit-for-Tat' (TFT), is extremely simple. The dilemma, you will recall, is to decide whether to cooperate or defect, but this time in a game proceeding over an indeterminate number of rounds. In TFT, you cooperate in the first round and in every subsequent round you repeat the behaviour of your partner in the last round. If your partner defects, you defect next time; if your partner cooperates, you cooperate.

More recently, biologists have applied game strategies to models that allow an element of chance by introducing a 'mutation' in behaviour once in every hundred generations. This reflects the situation in real biological communities more accurately. TFT still succeeds, but only if a small number of TFT players are present at the start, and it leads to even greater cooperation (NOWAK AND SIGMUND, 1992), but with dangers. From time to time there are phases during which almost all members of the population cooperate or almost all defect.

Still more realistic modelling led to a variant of TFT called 'Pavlov', which corrects mistakes and allows the exploitation of unconditional cooperators. In Pavlov, players repeat their own last move if it brought a reward: if both players cooperated and were rewarded, then cooperate; if you defected, your partner cooperated, and so you were rewarded, then defect; if you both defected and received

no reward, then cooperate. The game was repeated over 10⁷ rounds, with 10⁵ mutant strategies introduced. Pavlov also generated prolonged periods of cooperation and defection, switching from one to the other quite rapidly, but with a clear trend toward increasing cooperation. After 10⁴ rounds, only 27.5 per cent of rounds exhibited cooperation, but after 10⁷ rounds 90 per cent of them did (NOWAK AND SIGMUND, 1993).

Game theory based on The Prisoner's Dilemma provides powerful insights into the evolution of cooperation in a wide variety of contexts. Mutualism, for example, in which members of two different species perform services for one another, had long puzzled biologists. Why does a large fish not swallow the cleaner fish that moves about inside its mouth picking food from its teeth? The mathematics of the relationship demonstrate that cooperation is an ESS and mutualism is not subverted by occasional cheating (HAMMERSTEIN AND HOEKSTRA, 1995).

Persuasive though it is, the model remains somewhat controversial, and although examples have been found of behaviour that supports it, there are also some that seem to refute it. Lionesses, which cooperate in pairs to repel strangers seeking to invade their territory, may be brave or cowardly. Two brave lionesses will advance together, sharing equally the not inconsiderable risk of injury when the invader is encountered. If one of the pair is a coward, she will hang back. The brave lioness will advance more slowly, glancing behind her to see what her companion is doing, but apparently tolerates this cheating, because in subsequent forays to repel intruders the brave individual does not hang back herself and makes no attempt to punish her cowardly companion in a 'tit-for-tat' way. It is possible that relationships among lionesses are complex, involving much more than the shared defence of territory, and cowards contribute to the welfare of the group in other ways that warrant toleration of them, but in this case at least it seems the model strategy is not being applied (MORELL, 1995).

Cooperation is only one aspect of behaviour that can now be modelled mathematically to discover evolutionarily stable strategies. Natural selection favours those individuals that use their time and resources most efficiently. The dawn chorus of birds, for example, occurs because at first light the birds cannot see well enough to allow them to forage for food, so they can afford to spend time declaring their territories.

Later, when they start foraging, they are likely to adopt an optimum foraging strategy, which can also be calculated. In Figure 5.4, the heavy curve shows the amount of food, as energy, that the forager accumulates during the time spent foraging. The diagonal straight lines connect the time at which the forager starts to travel from one foraging patch to the next with the point on the



Figure 5.4 Optimum foraging strategy

heavy curve corresponding to time at which it leaves that patch. The intersections of the diagonal lines with the heavy curve indicate the amount of food energy actually gained during the time spent in a patch. It is important to remember that the figure implies nothing about the physical size of patches: they are all assumed to be of the same size and quality. The steeper the angle at which the diagonal lines rise, the more rapidly the forager obtains food energy. Obviously, the more time the forager spends in a patch the more energy it gains in total, but there is very little difference in the rate of gain between spending a very short and very long time in a patch. The most efficient use of foraging patches requires the forager to spend an intermediate length of time in each. This optimizes its foraging strategy by providing the most rapid acquisition of food. It is not too difficult to see why this should be so. When the animal first enters a patch the most palatable and nutritious food items are relatively abundant. It eats well, but with each item it consumes the total number of items is reduced and so it must spend more time looking for them. Its rate of energy acquisition slows. If it spends a very short time in a patch it will not be there long enough to acquire very much food, but if it stays in the patch a very long time an increasing proportion of time will be spent searching for items, and as the more nutritious items are consumed the nutritional quality of the patch as a whole will diminish. The optimal strategy, therefore, is to take the most palatable items quickly and when they are gone move to another patch. Such optimal foraging behaviour has often been observed. Similar optimal strategies can be devised for many behaviours (COCKBURN, 1991, pp. 88–94).

Behaviour is subject to natural selection. This applies to human behaviour as much as to the behaviour of any other species, but with a risk and an important difference. In non-human species variable amounts of behaviour are inherited. Web-spinning spiders do not learn to build webs, they inherit that ability, just as cleaner fish inherit their habit of foraging inside the mouths of particular large fish which they recognize as their 'customers', waiting in groups for them at 'cleaning stations'. Being inherited, such behaviour must be transmitted genetically and, therefore, behavioural genes must exist. Indeed, it was the idea that behaviour is to some degree determined genetically that gave rise to the scientific discipline of sociobiology. The risk is of extrapolating from this obvious link to the supposition that all behaviour results simply from 'programmed' instructions carried on genes. For spiders, worms, and other invertebrates this may be largely true, since they behave in highly stereotyped ways. Vertebrates show much more flexibility, however, and their behavioural responses to particular stimuli are not always the same. It is better to think of the genetic 'program' as supplying the capability for a range of behaviours. The resulting flexibility benefits the animals possessing it and is, therefore, favoured by natural selection, but the fact that it has evolved should not tempt us into the fallacy of extreme determinism.

The difference concerns humans. It is quite easy to demonstrate that our behaviour is also subject to genetic influence. Genes code for the synthesis of proteins and there are drugs that affect our moods or behaviour and are direct gene products (proteins) or the products of enzymatic reactions, and enzymes are proteins. Human behaviour is also flexible, and much more so than that of any other species because of our unique ability to contemplate the consequences of our actions, including their consequences for others. We can choose how we behave (TUDGE, 1993, pp. 100–105).

In recent years, unfortunately, press stories about 'homosexual', 'criminal', 'depressive', 'violent', 'alcoholic', and other genes have fostered a popular but misplaced belief in genetic determinism derived from neuroscientific research that has been reported out of context (ROSE, 1995). The truth is that very little is known about the link between genetic constitution and even physical differences between individual humans, let alone behavioural ones. Genetic determinism allows us to blame victims: people are poor because they are genetically disposed to idleness and feck-lessness or have inherited a low IQ. This leads to repressive political and social responses and, of course, to racism and gender discrimination.

48 Adaptation

Darwin based much of his evolutionary theory on his observations of domestic animals. He had a great fondness for pigeons and described the great variety of forms, all of which had been bred by pigeon-fanciers from the rock dove (*Columba livia*). Domestic dogs provide an even more dramatic example of the powers of selective breeding. From the Great Dane to the chihuahua, all are descended from a single species, the wolf (*Canis lupus*), and the entire process has taken no more than 12000 years (CLUTTON-BROCK, 1981, p. 34).

Genus	Species	Tree- feeding	Ground- feeding	Seed- eater	Insect- eater	Cactus- eater
Geospiza	magnirostris		Х	Х		
	fortis		Х	Х		
	fuliginosa		Х	Х		
	difficilis		Х	Х		Х
	scandens		Х	Х		Х
	conirostris		Х	Х		Х
Platyspiza	crassirostris	х			Х	
Camarhynchus	psittacula	Х			Х	
	pauper	Х			Х	
	parvulus	Х			Х	
Cactospiza	pallidus	Х			Х	
	heliobates	Х			Х	
Certhidea	olivacea				Х	
Pinaroloxias	inornata				X	

Natural selection takes longer, but produces similar results, albeit for different reasons. In his visit to the Galápagos Islands, a volcanic group some 800 km off the coast of Ecuador, Darwin noted a group of birds, clearly of similar general type, in which each species had a bill seemingly adapted for a particular diet. Known now as 'Darwin's finches' (see box), the group comprises 14 species (some biologists count 13, others 15, depending on the taxonomic criteria used), all of them descended from a single species that migrated to the islands from mainland South America. Figure 5.5 shows how they have diverged from the ancestral species. Some, with long, slender bills, feed on insects and nectar. Others eat seeds and have short, stout bills, the size and strength of the bill varying according to the particular seeds the bird consumes and the proportion of birds with large and small bills varying with the relative abundance of the foods to which they are best suited. The woodpecker finch, with a slender bill, does not hammer at wood and lacks both a long tongue and a very long bill with which it might extract grubs from beneath the bark. Instead, it uses twigs or cactus spines as tools (WILSON, 1992, pp. 93–95).



Figure 5.5 Adaptive radiation of Darwin's finches

Darwin's finches are adapted to the ecological niches they fill. 'Adaptedness' is the condition of being adapted, 'adaptation' the process by which adaptedness is acquired. In the case of the finches, adaptation occurred fairly rapidly when descendants of the ancestral population found a variety of food sources awaiting exploitation. Individuals with slightly thicker bills found seeds more suitable, those with slender bills fed preferentially on insects, and so the groups began to diverge. Rapid speciation of this kind, based on the colonization of under-exploited habitats, is called 'adaptive radiation'. It may occur at any taxonomic level. In the Galápagos Islands, there was an adaptive radiation of species; during the early Cenozoic Era, following the mass extinction marking the end of the Cretaceous Period 65 million years ago, there was an adaptive radiation of mammalian orders. An explosion of adaptive radiation at the species level even greater than that of the Galápagos occurred in Hawaii, another group of volcanic islands that was once devoid of life. There, a single species of finch produced 47 species and one or two groups of fruit fly (*Drosophila*) evolved into more than 600 species, one-quarter of all *Drosophila* species. Eventually, of some 21000 species of algae, protists, fungi, plants, and animals on the islands, more than 8500 occur nowhere else (MLOT, 1995).

Adaptation is driven by natural selection, because those individuals most suited to the conditions under which they live will produce most offspring, and these will inherit the characters that favoured their parents. Adaptedness, then, is a product of natural selection. This can lead to confusion between the terms 'adaptedness' and 'fitness'. Adaptedness is the ability to live and reproduce in a particular environment It is absolute, in that a species either possesses or lacks it. Fitness, in the Darwinian sense, is a measure of the degree to which the particular genetic constitution of an individual (a genotype) contributes genetically to the succeeding generation. The term applies to genotypes and it is relative, because it can be described only by comparison with the fitness of another genotype (PATTERSON, 1978, pp. 57–58). Some biologists prefer the term 'adaptive value' to 'fitness'.

Related organisms have adapted evolutionarily to varying environmental conditions in ways that now make them very distinct. In the last century this led zoologists to propose general rules describing differences that may be ascribed to temperature adaptation. Bergmann's rule (proposed in 1847 by C.Bergmann) states that animals in cold regions are larger than related forms in warm regions. This may be due to simple geometry: the larger the animal the smaller its surface area in relation to its volume and, therefore, the more efficiently it conserves heat.¹ The wing span of puffins (*Fratercula arctica*) reflects this rule; it averages 14 cm in the Balearic Islands, 16.5 cm in the British Isles, and 19 cm in northern Greenland (BERRY, 1977, p. 30). Gloger's rule (proposed by C.W.L.Gloger) states that animals in warm climates are more darkly coloured than those in cold climates, perhaps because they produce more of the dark pigment melanin. Allen's rule (proposed in 1876 by J.A.Allen) states that projecting parts of the body, such as ears, muzzle, and tail, tend to be longer in animals living in warm climates than in those living in cold climates, perhaps because heat is readily lost through them. There are exceptions to all these rules and their status as rules is dubious, but there are also many examples of the adaptations they describe. Arctic foxes (*Alopex lagopus*) have small ears and average 57 cm in body length (excluding the tail); red foxes (*Vulpes vulpes*) of temperate latitude have markedly larger ears and average 66 cm in body length; and fennec foxes (*Vulpes zerda*) of North Africa and the Near East have very large ears and a body averaging 39 cm in length. The biggest of all bears is the polar bear (*Thalarctos maritimus*), up to 2.5 m in body length; the American black bear (*Ursus americanus*) grows up to 1.8 m. Clearly, animals do adapt to climate physiologically, giving some support at least to Bergmann's rule.

Plants also adapt. Mangroves grow in, and also trap, salty, anaerobic mud along tropical coasts. Their roots require air and three genera have evolved root systems to cope with different levels of tidal flooding, illustrated in Figure 5.6. *Sonneratia*, which grows below the low-tide line, has



Figure 5.6 Adaptation by mangroves to different levels of flooding

'peg' roots; the main root lies just below the surface and has vertical extensions that project high enough to be clear of the water except at high tide. *Rhizophora*, which grows in the intertidal zone, has 'stilt' roots that are exposed to the air for much of the time. *Bruguiera*, growing in mud that is flooded only at high tide, has 'knee' roots: horizontal, underground roots with loops that project upward well clear of the surface.

It is not only climate and physical aspects of the environment to which species must adapt. Environments include other species and they also adapt to those. Perhaps the most convincing demonstrations of such adaptations are provided by mimics. It was the English naturalist Henry Walter Bates (1825–92) who, in 1862, first drew attention to species of moths that are palatable to birds, but which closely resemble other, unpalatable species and are avoided by predators. This is now known as Batesian mimicry and its best-known exponent is the viceroy butterfly (*Limenitis archippus*). It is edible, but is virtually indistinguishable from the monarch (*Danaus plexippus*), although it is somewhat smaller. The monarch concentrates in its body poisons produced by the milkweed plants on which its larvae feed. These induce vomiting within a few minutes, so any bird eating a monarch learns to avoid butterflies of its appearance. That appearance also protects the viceroy, but it works only as long as monarchs heavily outnum-ber viceroys. Were viceroys to become common, it would take birds longer to encounter a monarch, during which time they would consume viceroys, and they might not learn avoid-ance. Monarchs and viceroys are not unique. Many butterfly species are protected by accumulating poisons from the poisonous plants on which they feed and also have Batesian mimics.

Poisonous or otherwise dangerous species can also benefit by resembling one another. This type of mimicry is called Müllerian, after the German zoologist Fritz Müller (1831–97) who was the first to describe it, in 1879. Predators learn to avoid all species resembling the first distasteful one they encounter.

Mimicry has offensive as well as defensive uses. Some spiders of the genus *Myrmecium* are almost indistinguishable from the ants on which they prey. Spiders have eight legs, of course, and insects six, but the ant-mimics have the first pair of legs greatly lengthened and hold them so they look like antennae. One Red Sea species of blenny exploits the Batesian mimicry of two others. *Meiacanthus* has fang-like teeth that inject venom and predators learn to avoid it. *Ecsenius* is harmless, but is avoided because of its close resemblance to *Meiacanthus*. *Plagiotremus* resembles the other two and is also harmless, but feeds on the skin of fish that allow it to approach, supposing it to be both harmless and inedible (BURTON AND BURTON, 1977. p. 73).

This is called 'aggressive mimicry', and predators and parasites that are aggressive mimics may resemble their prey or hosts. There are species of fireflies, for example, which mimic the flashes, different for each species, by which males locate females and on reaching the females, eat them. The sabre-toothed blenny (*Aspidontus taeniatus*) closely resembles the cleaner wrasse (*Labroides dimidiatus*); when wrasse customers approach it to be cleaned it bites pieces from their fins. Many predatory mantids mimic the flowers on which they rest and capture insects attracted to the 'flower'.

Camouflage is not classed as mimicry, although camouflaged species often resemble the background against which they rest. It is not difficult to see how natural selection must favour well-camouflaged organisms, because camouflage will protect prey species from predators and increase the efficiency with which predators capture prey. It is not surprising that camouflage is very common. Not all species use coloration for concealment, however. Bright colours may also deter predators if they are associated with danger or unpalatability and it is this use of coloration that allows Batesian mimicry to evolve.

Natural selection provides a wholly adequate explanation for the vast range of shapes, colours, and behaviours we see around us. Heritable characteristics have adaptive value (increase fitness) if they enable certain individuals to withstand better than others the physical extremes of their environment, or provide them with shapes or colours that improve their chances of eating while reducing the chance of being eaten. Those individuals will produce more offspring and so their small, advantageous differences will be emphasized and become more widespread. This is how adaptation proceeds and how adaptedness is acquired.

49 Dispersal mechanisms

Opportunist plants that spring up within weeks when ground is cleared are able to arrive so quickly because their abundant seeds are light and carried on the wind. They are a familiar sight, floating past on their 'parachutes' of fine, white hairs. Maples produce one-winged seeds (sama-ras) that whirl like helicopter rotors, their spinning motion carrying them further than they would travel were they simply to fall. There are winged seeds that glide, and bladder senna (*Colutea arborescens*), a Mediterranean shrub, produces small seeds inside hugely inflated pods which float on the air like balloons. Tumbleweeds break off at ground level when their seeds have ripened and roll with the wind, sometimes for long distances, scattering seeds as they go.

These seeds are visible. Others are so small as to need no assistance in remaining airborne. Orchids produce microscopically small seeds comprising only a few cells, but some species produce a million of them at a time. Fungi release clouds of tiny spores.

There are plants that drop their seeds into flowing water and many produce seeds that are distributed by animals. Burrs are inedible fruits covered with small hooks by which they cling to the fur or clothing of any animal brushing against the plant. By the time they fall off and the fruit decays to release the seed, they may be a long way from their parent plant. The carrying of seeds on the outside of an animal is called 'epizoochory'. 'Endozoochory', the transport of seeds inside animals, is achieved by concealing a tough, indigestible seed inside a delicious fruit. When an animal eats the fruit it is rewarded with food, but the seed passes unaffected through its digestive system to be deposited in faeces, which also supply nutrient for the young plant. Fruits such as grapes, cher-ries, and dates that have thin skins, no smell, and are attached fairly firmly to the plant have evolved to be eaten by birds. Those adapted to attract other kinds of animal drop to the ground and often have thick skins concealing the edible parts and a strong, sometimes rancid, smell.

Many animals assist plants unintentionally by collecting seeds and storing them for future consumption. This is called 'synzoochory' and it works because although some of the seeds are eaten, many more are buried and never recovered. In effect, the hoarders sow them.

All organisms must disperse their offspring. A seed of a perennial plant deposited very close to the plant that produced it might germinate, but it would be unlikely to develop into a healthy plant, because of competition from its well-established parent. The young must leave home, and most plants, as well as fungi and many animals, achieve dispersal by broadcasting seed, spores, or fertilized eggs. These are known collectively as 'disseminules', because they are disseminated. This is passive dispersal, a random and very wasteful process. During the whole of their lives, a pair of sexually reproducing organisms need produce only two viable offspring to ensure their own replacement, yet broadcasters release vast numbers of disseminules, each of which cost energy and materials to produce. Production has to be prolific, because the parent has no control over the fate of its disseminules and most will fail to develop.

Dispersion is not the same thing as migration. 'Migration' generally describes the mass movement of organisms from one place to another, as when birds migrate between winter and summer locations. Dispersion, or dispersal, is the movement of individuals away from one another.

Passive dispersion is not necessarily truly random, because prevailing winds or the flow of water will tend to transport disseminules in predictable directions. Few passively dispersed disseminules travel far, their distribution forming the kind of pattern shown in Figure 5.7. This is what you might expect, because they begin falling to the ground from the moment they are released, but there are exceptions. Once airborne, disseminules and adults can be carried to considerable height and transported a long way.

Some species of spiders, in particular, exploit this possibility. They disperse by 'ballooning'. A young spiderling climbs to the top of a plant or fence, turns to face the wind, then raises its abdomen and releases a stream of silk from its spinnerets. The silk rises, the spider releases its grip, and the wind carries it where it will. The spiderling may need to produce several strands of silk before one lifts it into the air and the abandoned strands left by thousands of spiderlings can cover vegetation as 'gossamer'. If, on a warm summer evening, you find tiny spiders in your hair or on your clothes they are likely to be ballooning spiderlings. Most of the spiderlings drift at heights below about 70 m, but they have been found in samples of 'aerial plankton' taken at 3000 m and they can sometimes be carried for hundreds or even thousands of kilometres (PRESTON-MAFHAM AND PRESTON-MAFHAM, 1984, pp. 99–101).

As you will appreciate if you have watched swallows or bats feeding on airborne insects (and spiderlings), the air can be quite densely populated. Years ago, a study in England counted 12.5 million insects an hour drifting through a rectangle 91 m high and 1.61 km long (KENDEIGH, 1974, p. 278). Hurricanes can carry mainland organisms to remote islands, and tornadoes have been known to raise aquatic animals, including fish, and drop them somewhere else. Most die, of course, but occasionally some may fall into water and so colonize a new lake or river.

Larger animals also disperse, and although these animals are independently motile their movements are usually random. They simply move away from the area occupied by their parents in search of a patch of habitat where they will experience less competition. Their travels seldom take them beyond the borders of the range their population inhabits and those which do cross the border may find themselves in an inhospitable environment where they cannot survive.



Figure 5.7 Common pattern for passive dispersal

There are exceptions. Some marine invertebrates, for example, which spend their adult lives anchored to a particular spot and feed by filtering particles from the surrounding water produce large numbers of motile offspring. These live as juveniles among the plankton, but actively seek sites that are likely to provide them with a substrate on which they can settle securely and where food is likely to be abundant. Their dispersal is certainly not random. Nor is that of some of the species described in the next section, headed 'Wildlife species and habitats'.

It may happen, however, that a disseminule or young animal wanders beyond its ordinary range and into a site, previously unoccupied by members of its species, where it finds the resources it needs. This allows it to expand the range of its species by diffusing into an adjacent area. Daisies quickly establish themselves in new lawns by this type of range expansion.

Species can expand their ranges by diffusion only if their original ranges are adjacent to favourable areas, and eventually their expansion will be halted by a barrier. This may be physical, such as sea for terrestrial species or land for marine species, a desert or mountain range, or biological, such as an entirely different type of vegetation. Barriers isolate populations, but occasionally they disappear and sometimes they can be circumvented. Geologic processes can cause sea levels to change, creating or removing barriers. At one time, species could move between the Old and New Worlds across the land bridge linking Alaska and Siberia across the Bering Strait, and before the Atlantic Ocean opened North America and Eurasia were part of the same landmass. Less than about 8000 years ago Britain was joined to continental Europe by a bridge between what are now Hull and the Dutch archipelago and Esbjerg, Denmark, and across what is now the English Channel (SIMMONS *ET AL.*, 1981, pp. 86–88).

Species sometimes cross or circumvent barriers. Air currents may carry them across mountains as seeds, and small animals occasionally drift to sea on rafts of vegetation washed away by storms. Even more rarely, they make landfall on an island they can colonize. Insects, spiders, birds, and bats can be blown long distances. Such long-distance travellers seldom survive for long. It is fairly common for North American birds to be blown across the Atlantic, but they arrive in Europe singly and so cannot breed, and in any case find themselves in well-populated habitats with few niches awaiting definition, a fate they share with most dispersing individuals that stray beyond the borders of their established range.

When exceptions occur the result can be spectacular and 'jump dispersal' (BREWER, 1988, p. 37) can be highly successful. It most commonly results from the deliberate or accidental introduction of species by humans into regions where food is abundant and predators and parasites are left behind. 'Tramp' species are carried inadvertently; they 'hitch rides'. That is how the brown rat (*Rattus norvegicus*) and house mouse (*Mus musculus*) have travelled the world and it is how the water hyacinth (*Eichhornia crassipes*) first established itself in Louisiana (see box).

Introduced species

Species introduced to a region may not survive, but if they do their numbers may increase until they present serious economic or ecological problems. They proliferate because the environment in which they establish themselves does not include the predators and parasites that restricted their numbers in the environment from which they came.

Once established, exotic species may become fully naturalized to their new environment and, eventually, so familiar as to be often regarded as native. They may still make nuisances of themselves, however. The house mouse

(*Mus musculus*), originally a native of the Middle East, was possibly the first mammal to be introduced to Britain by humans, in pre-Roman times. The black rat (*Rattus rattus*) probably arrived in Britain in the eleventh century and the first brown rat (*Rattus norvegicus*) arrived early in the eighteenth century. The domestic cat (*Felis catus*) was present in Britain by the Middle Ages and has been introduced deliberately to places from which it was previously absent, usually to control rodents. Many have escaped or been driven from human homes and established a large feral population that has a marked effect on populations of the small mammals and birds on which cats prey.

The rabbit, introduced to Australia in 1787 and 1791, bred more rapidly than native marsu-pial animals and adapted equally to semi-arid and humid regions until its consumption of grass and crops caused serious economic loss to farmers. Foxes, introduced as predators, preyed on native marsupials and birds rather than rabbits, devastating their populations.

Exhibitors travelling from Venezuela to the Cotton Exposition held in New Orleans in 1884 took with them specimens of an attractive aquatic plant, the water hyacinth (*Eichhornia crassipes*). It escaped, established itself, and is now a serious weed of freshwater aquatic systems throughout the tropics. It forms huge, floating mats and can double its numbers every 8–10 days, choking navigable waterways.

Others are introduced deliberately. The European house sparrow (*Passer domesticus*) was introduced to North America in 1852–53 and is now widespread. As Figure 5.8 illustrates, the starling (*Sturnus vulgaris*), introduced to North America in 1890–91, expanded its range to more than 4 million km² within half a century (KENDEIGH, 1974, pp. 276–277).

Britain, too, has considerable experience of introduction. If you see a squirrel in Britain it is most likely to be a grey one (*Sciurus carolinensis*), which is much more numerous and widely spread than the red squirrel (*Sciurus vulgaris*). Indeed, the scientific name *vulgaris* is something of a misnomer, because there are now no red squirrels over large areas of southern England and it is certainly not common. As its name, *carolinensis*, indicates, the grey is not native to Britain. There may have been a few in North Wales early in the last century, but grey squirrels were introduced to about 35 sites in England, Wales, Scotland, and Ireland between about 1876 and 1929 (CORBET AND SOUTHERN, 1977, pp. 166–167). At first they spread rapidly and continue to do so more slowly.

Rabbits (*Oryctolagus cuniculus*), now so common throughout Britain, were also introduced. The earliest unambiguous reference to them dates from the thirteenth century and they were abundant in England by the sixteenth, but it was not until the eighteenth that they spread throughout Wales and the nineteenth that they reached most of Scotland (THOMSON AND WORDEN, 1956, pp. 12–13).

As the spread of the rabbit shows, a species may establish itself but still take a considerable time before managing to expand its range by diffusion. The grey squirrel was fortunate in that its principal competitor, the red squirrel, is subject to wide fluctuations in numbers, and as it declined the grey was able to occupy and retain its habitat. The expansion of the rabbit, originally raised for food in guarded warrens, may have been due to agricultural changes that involved enclosing open land with hedges that provided shelter.



Figure 5.8 Expansion of the European starling's range In North America 1915–50 Source: Kendelgh, S.Charles. 1974. Ecology with Special Reference to Animals and Man. Prentice-Hall, Englewood Cliffs, NJ

Ecologists usually oppose the introduction of species to new regions, because of the havoc such introductions may cause should the species succeed in its new habitat. The competitive exclusion principle, according to which no two species (or groups of species) with identical resource requirements can survive together in the same ecosystem, strongly suggests that an introduced species can succeed only at the expense of native species. This is not inevitable, but there are enough examples to justify caution.

50 Wildlife species and habitats

If you were looking for badgers, there are certain kinds of places it would be worth visiting and others you could ignore. You would be wasting your time searching in a low-lying, wet field. Badgers do not live in such places. The best place to look for signs of a set might be in deciduous woodland, especially if there were fields nearby used for pasture and arable crops. Together, the woodland and fields would provide badgers with abundant food and a varied, balanced diet. You might call it a good badger habitat.

A habitat is a place, an area in which an organism lives, feeds, and breeds. It is sometimes described as the organism's address. Within its habitat, the organism lives in a certain way peculiar to its species. This is its niche. If the habitat is its address, the niche is its job.

Turn the concept around, and an area of land or water can be examined for the different habitats it provides. Over a large region of the world, the general type of vegetation, such as temperate grassland, tundra, or tropical rain forest, defines a biome, but clearly a biome contains many habitats. In most school atlases, the Amazonian rain forest is coloured a uniform shade of green, suggesting that a traveller traversing it would see little variety in flora and fauna over its entire 4 $\times 10^{6}$ km². Closer inspection of a 5 $\times 10^{5}$ km² area has revealed that far from exhibiting a tedious uniformity, the forest comprises a patchwork of 50 or so types of forest (CULOTTA, 1995a), visible in satellite images as patches of different colours identifiable on the ground as distinct vegetative formations (an observation atlas publishers may care to note). This discovery has profound implications for conservation in the region, because it shows that current efforts, based on identifying and protecting areas of significant biodiversity, rely on quite inadequate survey data (TUOMISTO, ET AL., 1995). Scientists do not use school atlases, of course! Their studies of changes in vegetation patterns over very large areas are based on satellite images (PARKINSON, 1997, Chapter 7) that reveal a considerable amount of detail, but require careful interpretation (TOWNSHEND ET AL., 1993). Habitats also have histories and some of their characteristics may have originated long ago. The great variety in the Amazon basin may have developed during the middle Miocene, about 10^6 years ago, when the interior of tropical South America was partly an inland sea, open to the Atlantic in the north, east (through what is now the Amazon River), and south. The Amazon Sea divided the land into a mountainous (Andes) western peninsula and two large islands, the Guayanan and Brazilian shields (WEBB, 1995).

Indeed, habitats can exist on a very small scale. A precisely defined portion of a larger habitat, where a particular species or community is most likely to be found, is called a 'microhabitat'. It is possible, therefore, to consider a main habitat as a mosaic of microhabitats, but with some species moving freely among them.

A pond may provide a habitat for various fish and aquatic birds. Ducks may feed on it and nest close to its banks, and herons may visit it to hunt for fish and other small animals. In more detail, however, the number of microhabitats it provides depends on the size of the organisms inhabiting them. The pond in Figure 5.9 is fairly typical. It has an island, where ducks and other birds probably roost and breed. Around the island the surface water provides a habitat for duckweed and all the small animals that feed on it. Further away, the bottom mud and water depth are suitable for waterlilies, so they have colonized that area. In several places near the banks, where the water is shallow, reeds have established themselves and other birds shelter among them. Dead branches and leaves floating on the surface provide habitats for other small animals, and gravel washed in from the stream feeding the pond provides conditions suitable for a quite different population. Crevices between the stones near one bank provide a habitat for insect larvae. Microorganisms also have 'addresses'. Their habitats are very small, of course, and the pond and its inhabitants provide an even wider variety of those.

Badgers often live in a woodland habitat, but within the woodland each individual tree is also not one habitat, but many. There are insect larvae that feed on its leaves and other larvae that feed on or beneath its bark. Birds feed on the larvae and roost and nest in its branches. In many countries, but not Britain, there are tree frogs that spend their entire lives in their arboreal habitats.

When plant seeds disperse, chance rules their fate. Those which land in favourable spots thrive, those falling on ground that is too dry, too wet, too warm, too cool, too exposed, or too crowded fail to germinate or, if they do germinate, soon die. Plants occupy habitats, they have 'addresses', but they cannot go looking for them. Most animals, on the other hand, do choose their habitats. An animal tours an area, being especially attracted to certain places by their physical appearance. Visits to those places allow it to examine the finer details of the accommodation and



Figure 5.9 Habitats In a pond

neighbourhood. If it finds food, suitable shelter, a nesting site, and the probability of attracting a mate, it may settle. If not, it resumes its exploration of the surrounding area.

Some years ago, the German ornithologists R.Berndt and W.Winkel monitored the preferences of young pied flycatchers (*Ficedula hypoleuca*). Some of the birds were hatched and raised in deciduous woodland, others in coniferous woodland. Of those raised in deciduous woodland, 69 per cent settled in deciduous woodland, and of those raised in coniferous woodland, 79 per cent settled in deciduous woodland. Clearly, those pied flycatchers preferred deciduous woodland even though some of them had not lived in it when young and, presumably, they settled in coniferous woodland only when they found the deciduous woodland overcrowded (BREWER, 1988, p. 33). They chose it.

We can imagine birds or badgers visiting possible sites and settling when they find one to their liking, but much smaller animals than these choose their habitats. Crop pests, such as aphids, occur on some plants but not others, yet aphids are weak fliers, carried this way and that by winds and thermal currents. They disperse as winged forms, but within an hour or two they cease to fly actively and begin to fall, possibly steering themselves towards plants that exhibit some promising feature. If it turns out that the plant suits them they stay, if not they take off again, if necessary making several flights during the limited time remaining before their wing muscles degenerate (JOHNSON, 1963). Their habitat selection is more haphazard than that of a bird or mammal and many individuals perish without finding the food they seek but, as every farmer and gardener knows, aphids are highly successful at the species level.

Habitat selection is a matter of locating resources and these may be of quite different types. Biting midges (*Culicoides* species), for example, breed in water. Their thin, worm-like larvae swim about in ditches, ponds, and wet soil, but the female adults, no more than 1–4 mm long, feed on bird or

mammalian blood, which contains proteins they need for egg production, and those notorious in parts of Scotland (and known in America as 'no-see-ums') favour human blood. They fly mainly in the evening and locate their victims by scent, taking full advantage of warm, sultry weather, when humans are perspiring (COLYER AND HAMMOND, 1968, pp. 77–78), but they cannot fly very far. Their habitat, therefore, must comprise suitable sites for egg-laying located close to places where humans congregate (and they are best controlled by identifying and destroying their breeding sites). Other species, of which there are about 800, specialize in the blood of different animals, and some tropical species transmit diseases (FREEMAN, 1973), the insects and the animals on which they feed comprising habitats for the parasites.

Habitats vary in size according to the species occupying them. For a species to survive, the habitat must support a population large enough to sustain itself by breeding. Should numbers fall below a certain threshold, some species lack the social stimulation to breed and their populations may collapse, even to extinction. This phenomenon was first described in 1949 by a team of ecologists led by W.C.Allee. Known as the Allee effect, it is believed to be what caused the extinction of the American passenger pigeon (*Ectopistes migratorius*). The minimum viable population (MVP) of any species is generally defined as that number which gives the population a 95 per cent chance of persisting for 100 years. This can be calculated by population viability (or vulnerability) analysis (PVA), and Figure 5.10 shows the result for mammals. Depending on the amount of variability over the area of the habitat, the graph shows, for example, that for a species with an average body weight of 1 kg (about the size of an adult hedgehog), the MVP is between about 8000 and 70000. MVP can then be used to calculate the minimum area of habitat that population requires. Herbivorous mammals require a smaller habitat than carnivores, but for a 1 kg mammal in temperate latitudes, a viable herbivore population needs between about 5 and 80 km² and a viable carnivore



Figure 5.10 Population size needed for a 95 per cent probability of persisting 100 years After Brewer, Richard. 1988. The Science of Ecology. Saunders College Publishing, Fort Worth, TX

population between about 50 and 1000 km², depending on the variability within the habitat area. The calculation is of obvious value in planning national parks and nature reserves.

Once established, a species can profoundly alter its habitat, with consequent effects on other species, but some species are more influential in this regard than others. Recognizing this gave rise in the 1960s to the concept of 'keystone' species, species that determine the character of the entire habitat by their presence or absence. It began when Robert Paine, an American marine ecologist, removed many individuals of a particular starfish species (*Pisaster ochraceus*) from the intertidal zone on a rocky shore. Mussels, the principal prey of the starfish, occupied the area and more than 300 other species, absent when the starfish was present, established themselves in the mussel beds. In the years that followed, more keystone species were identified. Keystone species are top predators and, although clearly important, they are not the only determinants of habitats. Among plants and microorganisms, species are now known to form 'functional groups', in which several species perform the same ecological function and one can be replaced by another. Ecologists are using this idea to develop 'patch models' of habitats in which varying ecological processes and relationships can be monitored (STONE, 1995).

Introduced species, often lacking the predators and parasites associated with them in their original habitats, can sometimes invade and disrupt habitats. Biologists distinguish between 'native' species that arrived by natural colonization in prehistoric times, 'naturalized' species that were introduced by humans but now maintain themselves without human intervention, and 'exotic' species that grow mainly or wholly because humans have planted and tended them. It is the naturalized species that can prove disruptive. Britain has only three naturalized and invasive tree or shrub species—sweet chestnut (*Castanea sativa*), introduced in Roman times; sycamore (*Acer pseudoplatanus*), introduced in medieval times; and the common rhododendron (*Rhododendron ponticum*), introduced more recently as an ornamental (RACKHAM, 1976, p. 19) —but there are several smaller plants, such as Japanese knotweed (*Polygonum cuspidatum*), that have become troublesome weeds and others that are in the process of becoming naturalized and invasive, sometimes with mixed results. *Buddleja*, for example, was introduced to Britain as an ornamental in the 1890s and by the 1930s was colonizing waste ground. It is now establishing itself widely. It has proved more attractive to butterflies than any native plant and by the 1980s a large variety of animal species were living in association with it.

Wildlife, the term embracing all undomesticated species (although some people confine it to animals), can be conserved in special locations, such as zoos and botanic gardens, but retaining it in the wild is preferable. This requires that habitats be protected, but if they are to survive, species must be provided with the full range of conditions they require. This means that before they can be protected habitats must be identified and analysed to determine their suitability. Once defined, they must then be managed to ensure they remain suitable, and one of the most important management tasks is the prevention of invasion by highly competitive, naturalized species. Rhododendrons, for example, are attractive, popular plants and people often object when conservationists cut them back quite savagely or even uproot them, but unless they were controlled, the invaders would quickly come to dominate the habitat and so destroy its value for many other species.

51 Biodiversity

At the United Nations Conference on Environment and Development (UNCED, also known as the 'Rio Summit' and 'Earth Summit'), held in Rio de Janeiro in the summer of 1992, governments agreed a Convention on Protecting Species and Habitats. Environmental groups and the press nicknamed it the 'Biodiversity Convention'. 'Biodiversity' is a contraction of 'biological diversity'.

At the most general level it refers to the variety to be found among living organisms throughout the Earth, and the Convention reflects the widespread public sentiment that this variety enriches the planet and our own cultures by virtue of its existence and the desire that so far as possible it should be maintained. Accompanying these feelings is the fear that in fact species are going extinct at a rate unprecedented in recent history and, therefore, the variety of organisms is being eroded. These views, and the fear, are shared by most biologists.

Unfortunately, translating this rather vague desire into practical policies for maintaining variety raises formidable difficulties. In the first place, we must agree on a definition of 'biodiversity'. We might take it to mean genetic diversity, the entire global gene pool. In that case, it is not only species we must preserve, but the genetic variations within each population of every species, possibly amounting to some 10⁹ different genes, of which we have limited knowledge of some of the 1 per cent that are expressed in the appearance of organisms (phenotypes) (PELLEW, 1995). Alternatively, we might seek to protect ecosystems by identifying and safeguarding each small area of habitat.

Most people are satisfied with an apparently less extreme requirement and define 'diversity' as 'species diversity', which is usually defined as the number of species in a particular area or community. In the case of biodiversity, it means the total number of species alive on Earth (ways of estimating diversity are outlined in section 42, headed 'Simplicity and diversity '). This requires us to prevent, so far as we can, the extinction of species. If we are to achieve this we must first determine the present rate at which species are going extinct and before we can do that we must know how many species there are.

There is an additional complication over the word 'species'. At one time this referred to a clearly defined concept. Literally, 'species', from the Latin *speculare*, to look, describes a group of organisms that resemble each other. Traditionally, taxonomists have applied the term to a group of organisms that are able to interbreed among themselves but are unable to breed with other groups. This is a useful definition, but it is not the only one. Nowadays a species defined in this way, by reproductive isolation, is usually called a 'biological species' or 'biospecies' for short.

The biospecies concept is essentially negative, in that it defines a species by the inability of its members to breed with non-members. A positive approach refers to the unique fertilization system that requires an organism to recognize as a mate only an individual sharing that fertilization system. In this definition, organisms mate specifically with members of their own species. This is known as the 'recognition species concept'.

Even so, the concept can be applied only to sexually-reproducing organisms. To expand it to asexual organisms there is a 'cohesion species concept'. It defines a species as a group of organisms that are genetically similar or comprise populations that are recognizable by their periodic increase and decrease in size.

Applying any definition based on reproduction requires fairly detailed and reliable knowledge of the behaviour of organisms and this may not exist. Increasingly, therefore, biologists are tending to use a 'phylogenetic species concept'. This defines a species as a group of organisms that share certain inherited physical characteristics not possessed in that combination by other organisms.

There are, however, groups of organisms that differ in form or structure—morphologically—from other groups, but without constituting a formal species. These are known as 'morphospecies'.

In discussions on biodiversity, 'species' usually means 'phylogenetic species'. This is seldom specified, however, and work is still continuing to develop a satisfactory definition of 'biodiversity'.

So far, about 1.6×10⁶ species have been described and of those fewer than 10⁵ are familiar, interesting, or pretty enough to have been studied in detail (PIMM *ET AL*., 1995). More are being discovered all the time. In 1988, two primates and one deer were discovered, another primate (a tamarin) was found in 1990, and since 1908 11 species of cetaceans (whales and porpoises) have been added to the global inventory, amounting to 13 per cent of all known members of that order (WILSON, 1992, p. 140). Between 1978 and 1987, the newly identified animal species were 5 birds, 26 mammals, 231 fish, and 7000 insects (PELLEW, 1995). Clearly, the species that have been found represent only a proportion of the total number, and estimating that number must necessarily involve an extrapolation from what is known to what is unknown. Many scientists have attempted the task, producing estimates of up to

 100×10^6 species, but a conservative and probably more realistic estimate puts the total at $5-10 \times 10^6$. Robin Pellew, director of the UK branch of the World Wide Fund for Nature, has taken a median estimate of around 8×10^6 , broken down as in Table 5.1 (PELLEW, 1995). The true total is likely to be higher, because the list omits a number of invertebrate groups, such as the annelids (worms), sponges (Porifera), and cnidarians (hydras and jellyfish). It also omits such plant groups as the ferns, mosses, and bryophytes. Further uncertainties arise from taxonomic disagreements between 'lumpers' and 'splitters' that can alter significantly the number of species recognized in certain groups.

	No decoribed	Estimate of total po		
Group	(thousands)	(thousands)		
	((
viruses	5	500		
Bacteria	5	400		
Fungi	7	1000		
Protozoa	40	200		
Algae	40	200		
Nematodes	15	500		
Molluscs	70	150		
Crustaceans	40	100		
Arachnids	75	600		
Insects	950	4000		
Vertebrates	45	50		
Higher plants	250	300		
Total	1605	8000		

Table 5.1 Number of species described and the likely total number

Species do not persist indefinitely. Indeed, it was the realization that fossils are the remains or traces of organisms no longer to be found alive that led to the development of our present understanding of evolutionary processes. Estimating the number of species existing at present as a proportion of all the species that have ever lived is difficult, but the plants and animals alive today probably constitute around 2–4 per cent of all the species that have lived in the last 600 million years (MAY *ET AL*., 1995, p. 4).

Extinctions have not been spread evenly. There is a general background rate at which species go extinct, but there have also been at least five mass extinctions in which 65–85 per cent (and at the end of the Permian Period, around 225 million years ago, 95 per cent or more) of all species disappeared. Background extinctions have little or no effect on biodiversity, because their rate is matched or exceeded by that of speciation, in which one species divides into two and thus increases the number of species. Nor do mass extinctions produce more than a temporary reduction in the number of species into the vacated niches. The extinction of the dinosaurs, for example, was followed by rapid speciation among mammals. Today, the number of land-dwelling species alive is about twice the average of the last 450 million years.

The fact of extinctions makes it possible to estimate the average lifespan of species within different groups. Invertebrate species are estimated to survive for around 11 million years, marine animals 4–5 million years, and mammals around 1 million years (MAY *ET AL*., 1995, p. 3).

Such calculations provide a context, albeit a very approximate one, within which present concerns about biodiversity can be placed. If we have at least an idea of the number of species present, of that number as a proportion of all species that have ever lived, and of the rate at which species inevitably go extinct within different groups, we are in a much stronger position to address those concerns.

Species are not distributed evenly throughout the world, so the next step is to identify those areas with the greatest diversity. As Figure 5.11 shows, the number of species in a particular area may vary in two ways. The area possesses resources which organisms utilize, and although no two species (or functional groups) can have a full range of identical resource requirements, there is a small amount of overlap. We might imagine, therefore, a fully exploited habitat that supports seven species (the top drawing in Figure 5.11). If the resource base increases (perhaps the area is enlarged to include essentially similar habitat nearby), the number of species can increase (middle drawing). The number can also increase, however, if the species themselves are more higly specialized, so the resource requirement for each is narrower (bottom drawing). This is the case in many tropical forest areas, where very high species diversity results from local resource specialization among many closely related species (mainly of insects).

Even when areas of high diversity have been located, it does not necessarily follow that all are equally deserving of immediate protection. Common sense suggests we should first protect the area with the greatest number of species, then the area with the next largest number, and so forth, but in this case common sense is an untrustworthy guide. If the species in the area with the highest diversity evolved only recently, then they will still be closely similar genetically. Another area, with fewer species, might well contain a much more diverse assortment of genes (PELLEW, 1995). If the aim is to preserve genetic diversity, the second area would be a better place to begin, despite being poorer in species.

Sensible conservation requires detailed surveys not only of habitats and their inhabitants, but of the genetic constitutions of those inhabitants. This is a task for molecular biologists, who isolate, multiply, and compare sequences of DNA. Molecular ecology, a subdiscipline of molecular biology, is now well established in its own right.



Within habitats, many species tend to occur in 'clumps', rather than spreading themselves evenly. Animals which can choose their own habitats settle first in the area that suits them best and their

Figure 5.11 Species richness

numbers increase most rapidly inside that area. This is the 'core area' for that population and, as Figure 5.12 shows, it is surrounded by a wider area, more sparsely populated, from which individuals migrate into the core area as opportunity affords. This outer area is, therefore, a source area for individuals, but the rate of population increase is lower there than in the core area. Beyond that again there is an even more sparsely populated area, containing a 'sink' population of individuals that have moved away from the core area, perhaps because old age or illness renders them incapable of holding their own against more vigorous competitors. There is no population increase within this area. If part of the overall habitat is to be protected, but not all of it, so far as that species is concerned the core area is of greatest value and the outermost area can be sacrificed with little loss.

This much is obvious, but it can happen that owing to earlier disturbance of the habitat, the population is not where it would most like to be. The original core area may have been lost and the population is now elsewhere or distributed among several core areas each of which is inferior to the original one, and populations in some of these areas may survive only because they are periodically renewed by immigration from the other areas. Simply fencing off the entire area may be insufficient to halt a decline in the total population unless the original core area is first located and restored. Animals reintroduced into a habitat are more likely to survive and increase in number if they are released into the core area than the periphery (LAWTON, 1995).

So much is uncertain that all predictions of future extinction rates must be treated with great caution. Over the last few centuries, human activities, especially habitat destruction, have been the principal causes of present extinctions, but other factors are also involved. Madagascar, for example, has one of the most diverse populations on Earth, including 10000 plant species, more than half of all chameleon species, and many primitive primates, yet a few thousand years ago it



Figure 5.12 Range and population increase

accommodated far more species than it does now. It was widely assumed that many of the lost animals were hunted to extinction by early human colonists. There is now reason to suppose that humans arrived during a time of increasing aridity, when habitats were already shrinking, so although the human effect was additive, it is likely that climate change alone would have caused the extinction of many species (CULOTTA, 1995).

Since 1600, 485 species of animals and 584 of plants have gone extinct. At present, the IUCN (International Union for Conservation, Nature and Natural Resources) lists as 'threatened' 3565 species of animals and 22137 of plants (MAY *ET AL.*, 1995, p. 11). Some of the threatened species will certainly disappear, but not all of them. Recent rates of extinction have been calculated as between 20 and 200 species per million years (E/MSY). Were all the threatened species to vanish within less than a century, this rate would increase to 200–1500 E/MSY (PIMM *ET AL.*, 1995), which seems incredible.

Such a high rate of extinction would catastrophically reduce global biodiversity. It is unlikely to be so extreme, but nevertheless it is evident that much biodiversity will be lost unless positive steps are taken to prevent it. Before effective steps can be taken, however, a great deal of surveying remains to be done.

52 Fisheries

Fishing is the only form of hunting on which we continue to rely for a significant proportion of our food and, like hunters of old, we are beginning to quarrel on the hunting grounds as rival tribes compete for what appear to be dwindling stocks. In 1994, fishermen from France and Cornwall came to blows with Spanish fishermen in the Bay of Biscay where both groups were hunting tuna. The Spanish fishermen maintained that their traditional fishing method, using poles and lines, allowed them to catch bigger and better fish and that the French and Cornish boats, using drift nets they claimed exceeded the maximum length permitted in European Union waters, were catching smaller and therefore younger fish and so depleting the breeding population. The drift-netters replied to this that their nets were within the legal length, albeit only just, once allowance was made for the wide gaps between sections of net to allow marine mammals, such as dolphins, to pass. The real issue is more likely to have been the fact that by using drift nets the French and Cornish boats could catch three times more fish while employing half the number of fishermen.

Should this have been an issue? In a world claiming commitment to market economics are we entitled to criticize those who exploit technology and labour efficiently? Does it matter that so many Spanish coastal villages are economically dependent on fishing? The Cornish boats came mainly from Newlyn, which is no less dependent on fishing (and, ironically, most of the tuna landed in Britain is exported to Spain). It is hardly surprising that the quarrel became so bitter.

It erupted again a few months later, this time on the other side of the Atlantic, when the Canadians prevented Spanish boats from fishing for Greenland halibut (*Reinhardtius hippoglossoides*, in some reports incorrectly called 'turbot' by some British newspapers) on the edge of the Grand Banks. This is a large area, comprising a number of separate banks, south-east of Newfoundland, where the cold Labrador Current, flowing south, meets the warm Gulf Stream, flowing north. The resulting conditions favour plankton on which vast quantities of fish feed. The value of the Banks has been recognized ever since they were discovered by the Venetian navigator John Cabot (Giovanni Caboto) in 1497. Most of the Banks lie within Canadian territorial waters, but the Spanish boats were working on the small area that is in international waters. The Canadians argued that the Banks comprise a single,

unified resource from a biological point of view and, since almost the whole resource was indisputably Canadian, they were entitled to protect it from over-exploitation even if this meant interfering with

the right of fishermen to work in international waters. The Canadian action was illegal and placed friendly European governments in a difficult position, but in Cornwall Canadian flags were flown from so many fishing boats and public buildings that extra flags had to be imported from Canada and the Canadian High Commissioner visited the fishermen to thank them.

Less attention was paid to other disputes, but there were plenty in 1994. Icelandic gunboats were used to repel Norwegian trawlers. Fishermen were hurt in a disagreement between China and Taiwan over the waters around the island of Quemoy in the Taiwan Strait. Britain argued with Argentina over fishing rights around the Falklands (Malvinas). Namibia complained that EU vessels were taking lobsters in the Gulf of Aden.

When people warn of wars over resources, oilfields are what they usually have in mind, but serious disputes, if not literally warfare, have been occurring over fisheries for more than 20 years. It was in the 1970s that Iceland banned foreign vessels from fishing in waters over which it unilaterally claimed sovereignty. This led to three 'cod wars' between Britain and Iceland (ALLABY, 1977, p. 311).

Figure 5.13 illustrates the problem. Since 1972, the total world catch has increased by about 50 per cent, but it is based on a rather small number of species. As Table 5.2 shows 2, 20 species of marine and freshwater

Table 5.2	The	20 most important
species in	the	world's fish catch,
1995		

Species	%
	of total
Anchoveta	20
Chilean jack mackerel	12
Alaskan pollock	11
Silver carp	6
Atlantic herring	5
Grass carp	5
Common carp	4
Skipjack tuna	4
Chub mackerel	4
South American pilchard	3
Yesso scallop	3
Atlantic cod	3
Bighead carp	3
Largehead hairtail	3
European pilchard (sardine)	3
Yellowfin tuna	2
Pacific cupped oyster	2
Japanese anchovy	2
Atlantic mackerel	2
Caplin	2



Figure 5.13 World fisheries catch (marine and freshwater) 1972–92 (millions of tonnes)

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fish accounted for 38 per cent of the 1995 total world catch (of 112.9 million tonnes) and three species—anchoveta, Chilean jack mackerel, and Alaska pollack—accounted for 16 per cent of the world total, or 18.3 million tonnes.

Nor are the fish catches distributed evenly. China is the biggest fishing nation by far. Counting catches of marine and freshwater fish and farmed fish, in 1996 it produced almost 32 million tonnes, which is 26 percent of the world total. Between them, and in descending order of production, China, Peru, Chile, and Japan produce 45 per cent of the world's fish (GILL, 1999).

Carrying capacity and yield

The number of individuals of a given species that can survive in good health in a specified environment without degrading that environment is the carrying capacity for that species in that environment. Obviously, it varies from species to species and from one environment to another.

Each breeding season (usually, but not necessarily, 1 year) new individuals enter a population. Some are born and some arrive as migrants. If the number of these individuals exceeds that of those which die during the same period, the recruits represent a net increase to the population. If they are harvested, the size of the population remains unchanged. This number is the maximum sustainable yield (MSY) for that population in that environment.

In practice, harvesting the MSY will lead to a population decline, because recruitment varies from season to season, but for harvesting purposes the MSY figure must be calculated in advance. Since it represents a maximum, lower recruitment in some seasons will cause it to over-estimate the size of the harvest that can be taken safely.

The optimum sustainable yield (OSY) allows a wide safety margin. It is usually calculated as half the carrying capacity.

Yield quotas for commercial fisheries are calculated as shares of the OSY allotted to individual fleets.

There is widespread concern that fish stocks may be unable to sustain so intensive a fishing effort, but estimates of the level of effort they might sustain are very uncertain. The maximum sustainable yield (MSY) for any harvested species is calculated as being equal to the number of individuals entering the population, by birth or migration, during the harvesting period, usually one year. Prudence requires an allowance to be made for unpredictable events that might deplete the population, so the optimum sustainable yield (OSY) is lower than the MSY based on the crude replacement rate. Recruitment into a population may vary considerably from year to year, so for many species an MSY is valid only for the year to which the data refer. This is especially so for fish, which experience good and bad breeding seasons, but it means that an OSY figure always refers to the past. It does not tell fishermen what they can catch next season, but what they should have caught some time ago. Consider the history of North Sea herring, for example. At one time this fishery underpinned many local economies but, as Figure 5.14 shows, it was never reliable. The stock (not the catch, note) was more than 2 million tonnes in the late 1960s, but within a decade had collapsed to little more than 100000 tonnes. Then, during the 1980s, it recovered.



Figure 5.14 North Sea herring stocks 1960–90 (millions of tonnes)

While the stock was declining it was widely believed that over-fishing was the cause of the depletion, but it is more likely that the fluctuation was mainly natural, though possibly exacerbated by fishing. Huge fluctuations in the South American anchoveta fishery are similarly due to natural population changes, in this case caused by El Niño events.

Clearly, a retrospective OSY would be of limited use even if it could be calculated with anything like precision, but it cannot. In order to calculate it, the size of the population and the rate of recruitment into it must be known and in the case of fish this is not usually possible.

In practice, an MSY figure is usually based on the carrying capacity, which can be calculated (BEGON *ET AL.*, 1990, pp. 583–587). Even so, estimates vary. For many years the annual global MSY was believed to be around 100 million tonnes (ALLABY, 1977, p. 315), but others calculated it as 200 or even 400 million tonnes (KUPCHELLA AND HYLAND, 1986, pp. 267–268). For what it's worth, the present annual catch, of around 113 million tonnes, is close to the earlier estimate of 100 million tonnes.

Fish continue to be caught by methods developed over many centuries. The hunt is, indeed, traditional. Hooked lines are still used, sometimes from the boat, as with Spanish tuna-fishing, mackerel handlining in British waters, and trolling, in which the line is trailed astern of the moving boat, and sometimes as long lines. Hundreds of metres long, these are baited and left in position for several hours, or overnight, weighted at one end and buoyed at the other. The trawl net is a bag, tapering from an end held open by 'otter boards' to a narrow 'cod end', that is towed through the water. A ring or seine net is a curtain-like net, with weights along the bottom and floats along the top, that is paid out to form a circle enclosing the fish. The seine net is converted to a purse seine by drawing together the edges so the caught fish are entirely enclosed within it. A drift net is a curtain, or series of curtains, that hang vertically and trap fish swimming into them. Figure 5.15 illustrates these main techniques.



Figure 5.15 Commercial fishing methods. A, Mid-water pair trawling. B, Ring (or seine) netting. C, Purse seining. D, Drift netting

It is not the techniques that have changed, but the scale on which they operate and the ancillary equipment that supports them. Modern fishing boats are big and powered by large engines, which allow them to store and tow much larger nets than were once used. In some cases (see Figure 5.15A and B) two boats can collaborate, allowing even larger nets to be used. A large purse seine net could contain St Paul's Cathedral, London, with room to spare and will catch an entire shoal of fish. This hunting power is augmented by sophisticated navigation equipment that determines the position of a boat to within a few metres and fish-finding equipment that locates shoals very precisely. Commercial fishing still depends on luck, but to a far lesser extent than was once the case.

Such power and technical sophistication are expensive. Fully equipped fishing boats now cost in the region of £500000 and consume a considerable quantity of fuel. So large an investment can be supported only by maximizing the catch. Modern fishermen, therefore, are compelled to travel far and land huge catches simply to meet the cost of their own operation. They are trapped finan-cially as firmly as the fish are by the nets. The rise in the global catch is thus a consequence of increased fishing power driven economically and it is no coincidence that certain countries are predominant. Those are the countries that choose to encourage investment in their fishing industries. By no means are all of them industrialized countries. Apart from China, the world's largest fishing nation, Peru, Chile, India, Indonesia, Thailand, and the Philippines are among the top 12.

The situation, then, is that hunters armed with extremely powerful weapons are pursuing an unknown amount of game. It is not possible that they will hunt any species to extinction, because as its numbers decline it will become economically impossible to pursue it and populations will recover. What is possible, however, is that the more popular species may be hunted to commercial extinction. Herring, once a cheap food eaten mainly by poor people, almost disappeared from British shops during the 1970s and although it has now reappeared it is no longer cheap.

Regulation is necessary if stocks, and hence the industry itself, are to be protected. It is based partly on technical limitations placed on the equipment used and partly on quotas. Drift nets, for example, should be no more than 2.5 km long within EU waters, and minima are set for mesh sizes. Quotas are also agreed for all commercially important species, setting the total allowable catch and then sharing it among fishing nations. Despite the inevitable squabbles, the system works up to a point, but until now its success has extended only to the boundaries inside which governments can exercise jurisdiction. It was much more difficult, often impossible, to enforce in international waters. Attempts to reach a global agreement on the management of fish and other marine stocks continued, without much success, from 1974 to 1982 at the protracted UN Conference on the Law of the Sea and again from 1993 to 1995. Agreement was finally reached in August 1995, when a treaty committing nations to the regulation of fishing in international waters won unanimous approval and was forwarded to the UN General Assembly for adoption (HOLMES, 1995).

If the fishing effort is reduced there is good reason to suppose that depleted stocks will recover. In some species, when population size falls below a certain threshold it suffers an increase in parasitism and predation which deplete it further, reducing the likelihood of its recovery. This is called 'depensation' and it is known to affect whales, leading to concern that it might affect fish as well as these marine mammals. Studies of a variety of commercially important fish species indicates that they, and possibly all marine fish, do not experience such depensatory declines, suggesting that even though populations are severely depleted their numbers will increase if they are allowed to do so (MYERS *ETAL*., 1995). If depletion were irreversible, it might be argued economically that fishermen should continue to hunt until it became commercially impractical to continue. If stocks can recover,

on the other hand, fishermen can be told that if they reduce catch sizes for several seasons, perhaps drastically, the population will recover and catches can be allowed to increase again.

There is an alternative to hunting. Just as hunted mammals were domesticated and gave rise to animal husbandry, so fish can be raised in captivity. Most European salmonids (trout and salmon) are raised in this way, and the success of the fish-farming industry has lowered the price of their products so that what were once luxuries are now within the reach of many more people. Bass and most flat-fish can also be bred and raised in captivity. Fish farming is also traditional, in that it has been practised for many centuries in some parts of the world, and its popularity is increasing. Its disadvantage is that its products are more expensive than wild fish that can be caught in large amounts. Wild salmonids are caught in small numbers, or individually, which is why they can be farmed economically (see box).

Aquaculture

Fish can be farmed by a variety of methods. Freshwater ponds may be stocked with herbivorous species, such as carp, and fed with organic material either directly or indirectly by adding fertilizer (traditionally human sewage) to stimulate the growth of aquatic plants.

A coastal area, such as a natural bay, may be enclosed by permanent nets. Within the enclosed area, a stock of fish is protected from predators and its food supply augmented. This method is similar to ranching.

The most intensive methods involve controlled fish breeding and the raising of fish at high population densities in closed ponds, each pond holding fish of similar age. The fish are fed a highly nutritious diet and water temperature is controlled, to promote rapid growth to marketable size. Salmon, which spend part of their lives in fresh water and part at sea, are bred and raised in freshwater ponds, then moved to cages in sheltered salt water.

As with all animals stocked at high densities, disease can spread rapidly, with devastating consequences, and hygiene is extremely important. Water used for aquaculture must be kept clean and fish excrement removed promptly. Accidental leakages can cause pollution, and accidental escapes of exotic species, chosen on commercial grounds, can disrupt native populations in adjacent waters.

Should the costs of commercial fishing cause fish prices to rise beyond a certain threshold, farmed species will become cheaper and begin to appear in the shops. It is not inconceivable that one day hunting will cease to be viable and the fish we eat will be produced on farms.

53 Forests

Despite the stone, concrete, ceramics, metals, and almost endless list of other materials on which we depend, wood is still one of our most important resources. We build and furnish our homes with it and many of us heat them and cook with it as well. It is estimated that wood is the main or only fuel

for 30–40 per cent of the people in the world (TOLBA AND EL-KHOLY, 1992, p. 165). Indeed, so high is dependence on fuelwood in the less industrialized countries that in the world as a whole slightly more fuelwood is produced than wood for industrial use (TOLBA AND EL-KHOLY, 1992, p. 166). Paper, cardboard, and much of our packaging is also made from wood. In 1997, the total world production of paper and board was more than 299 million tonnes (LAVALLÉE, 1999).

Forests (*www.fao.org/forestry/forestry.htm*) are of such importance that on economic grounds alone it is in our interest to manage them with care. Unfortunately, however, much of the land they occupy is capable of producing food, and throughout history forests have been cleared mainly to provide agricultural land. Today, as Figure 5.16 shows, the proportion of the total land area that is forested varies widely from one country to another. This is not an entirely fair way to consider the situation, because countries also vary greatly in size and population density. Russia, for example, has 57 per cent of the world's boreal forest and Canadian forests cover an area greater than that of western Europe, but in neither country do forests occupy so large a proportion of the total land area as they do in Japan. At the other extreme, Ireland, only 6 per cent of which is forested, has large areas that are unsuitable for trees.

It is still true that agriculture, in one form or another, remains the immediate cause of most deforestation. Shifting cultivation accounts for 45 per cent of all clearance of closed forest, commercial farming and grazing for a further 15 per cent each, dams and roads for 10–15 per cent, and forestry for 10 per cent. When allowance is made for planting, the net annual forest loss in the world as a whole is probably 11–12 million hectares. In the tropics, the drier and mountain forests are being lost much more rapidly than the rain forests (PERSSON, 1995). The losses are confined to the tropics, however. In temperate regions, other than the United States where the area is decreasing by about 300000 hectares a year, the forested area is increasing, and the area is increasing overall. In Europe forests are expanding by about 200000 ha a year and in Russia by 2 million ha a year. The expansion is due mainly to plantation forestry, but it involves no loss of natural forest. The decrease in the United States affects only plantation and areas of natural regrowth, not primary or old-growth forest (ALLABY, 1999, pp. 162–163).



Figure 5.16 Percentage of land area under forest in various countries

Shifting cultivation was once widely practised in temperate regions, but now survives only in the tropics. It is a system of subsistence farming that begins with the clearance of trees and shrubs from an area. Such timber as may be of use is taken and the rest is commonly burned, clearing the ground and fertilizing it with wood ash. Crops are then sown and cultivation continues until, after a few seasons, tree seedlings and other 'weeds' become too troublesome to remove and yields start to fall. The operation then moves to another site, where it is repeated. Cultivation proceeds as a rotation, visiting sites in turn. Ideally, each site remains undisturbed for about 12 years between cultivations. This allows time for secondary forest and other vegetation to re-estab-lish itself and the system can continue for many years with no serious depletion of soil fertility. Managed in this way, however, 1 km² of forest will support only about seven people (WHITMORE, 1975, p. 229). As demand for farmland intensifies, shifting cultivators have little choice but to use fewer sites and return to them more frequently. This leads to soil deterioration and the permanent disappearance of forest.

There is nothing new in the conflict between agriculture and forestry. At one time, most of the British Isles was forested. As the climate warmed during the early years of the present (Flandrian) interglacial, first conifers and eventually broad-leaved trees colonized the land. Figure 5.17 shows that from the time the climax forest was established until about three thousand years ago, oak (Quercus species) and hazel (Corylus avellana) were the dominant species over the largest area, with elm (Ulmus species) substituting for oak in the south-west of Wales and England and over most of Ireland, birch (Betula species) and pine (Pinus species) confined mainly to northern Scotland, and a smaller area dominated by small-leaved lime (Tilia cordata) in the Midlands and south of England. About 5000 years ago, there was a sudden and dramatic reduction in the amount of elm, called the 'elm decline'. Opinions vary as to its cause. Some authorities hold that the elm was destroyed by early farmers, who cut its branches to provide browse for their cattle, preventing the trees from flowering and producing the pollen from which past vegetation patterns are reconstructed. The decline is certainly associated with a proliferation of weeds typical of arable crops (RACKHAM, 1976, pp. 45–46). It may be, however, that the elms succumbed to disease. The 1970s outbreak of Dutch elm disease in Britain provides dramatic evidence of the speed with which disease can almost eliminate elms.

By AD 43, when the Romans invaded, the forest had been cleared from the lighter lands and farmers were starting to plough the heavier clay soils. During the centuries of their occupation, the Romans turned England into one of the most important agricultural countries in the empire, clearing vast areas of forest for the purpose. They also used timber for building and as fuel for the many industries they established. When the Anglo-Saxons arrived, after the Romans had departed, they inherited a land from which much of the primary forest had gone (RACKHAM, 1976, pp. 50–52) and was being replaced by a secondary regrowth of forest on uncultivated land. The Domesday survey of 1086 portrays a countryside perhaps more wooded than it is today, but with many villages having no woodland nearby and many places, especially in the east, where small patches of woodland were miles apart. Large areas of the country consisted of farms with patches of woodland, much as it has remained (RACKHAM, 1976, pp.61–65). Clearing continued in the centuries that followed and by 1350 probably no more than 10 per cent of England was forested, the same as the present-day figure for the United Kingdom. The later construction of the navy, in Tudor times, and the rise of the iron and steel industries still later actually had little effect (ALLABY, 1986, pp. 95–97).

Where forests and farms compete for land, confrontation invariably presents victory to the farmers, for the simple reason that the economic return from farms always exceeds that from forests. If necessary, the farmers can buy out the foresters. Yet forests are a vital resource. In Britain, the state forests are owned and managed by the Forestry Commission, established in 1919 with the task of
building up a strategic reserve of standing timber following the widespread felling that had occurred during the First World War, when timber imports were much reduced. The proportion of forests managed by the state varies, but national or federal governments manage at least some forests in most countries.

For many years, most Forestry Commission planting was of fast-growing conifers, sited on marginal land, usually in the uplands, that could be spared from agriculture. The relegation of



Figure 5.17 Tree cover in the British Isles about three thousand years ago Source: Rackham, Oliver. 1976. Trees and Woodland in the British Landscape. J.M.Dent and Sons, London

forests to marginal land caused problems. Trees demand growing conditions not much different from those required by many farm crops, so species were chosen that could survive the relatively harsh environment allotted to them and, to protect them from severe weather, they were planted in solid blocks. These were visually intrusive in landscapes from which the primary forest disappeared centuries ago and was never replaced, partly because the plantations were very dark in colour against the paler background of upland pasture and partly because of the severely geometrical shape of the blocks. It was also the practice to plant an entire block at the same time, so its trees were all of the same age, and harvest the timber by clear-felling the whole area, leaving the unsightly debris to scar the landscape until the succeeding crop grew up to hide it.

Modern forestry practice avoids these causes of very understandable offence. Trees are planted at intervals, producing stands of mixed ages that are harvested by removing much smaller blocks from within the forest. The edges of blocks are less straight, giving the forests a more natural appearance, and conifer plantations are often surrounded by broad-leaved species that produce a lighter, gentler colour.

More recently, the policy has been to plant rather more broad-leaved trees, especially in the lowlands of England and Wales, and to take much greater account of the wildlife importance of forests and their value for public recreation. The national forest will remain predominantly coniferous, however. Large 'community forests' are planned for several areas, sited to allow access from major population centres and intended primarily for amenity and wildlife conservation purposes, as well as the commercial production of timber.

Conifers produce softwood. In addition to its wide range of uses as timber, it is also used to make chipboard, fibreboard, and paper of all kinds. All paper is made from wood grown in plantation forests. Traditionally, broad-leaved forests were managed to produce timber for construction and shipbuilding and also smaller wood to make furniture and implements. When charcoal was an important fuel it, too, was produced from small wood. Selected trees were allowed to grow to their full size, as 'standards', to supply timber. The others were coppiced. This involved cutting them almost to ground level, leaving a stump, called a 'stool'. The section of Figure 5.18 shows on



Figure 5.18 Traditional tree management

the left the tree prior to cutting, in the middle the stool left after cutting, and on the right the appearance of a mass of thin shoots one year after cutting. With some species, the new shoots can grow more than 5 cm a day (RACKHAM, 1976, p. 22). Coppicing was practised rotationally, certain trees being cut each year, and about 12 years was allowed for the shoots to grow to useful size. Curiously, this apparently harsh management seems to prolong the life of many species. On more open sites, where trees were surrounded by pasture, they were more commonly pollarded, by cutting about 3 m above ground level to leave a 'boiling' from which the new shoots would grow. The effect was similar to coppicing, but pollarding protected the young shoots from damage by livestock. With some species, coppicing kills the stool but not the roots, from which new growth appears (the right-hand section of Figure 5.18). Coppicing has long been advocated by conservationists, for two reasons. By preventing most of the trees from growing to their full size and producing an almost complete canopy of leaves that shade the ground, coppicing allows sunlight to penetrate to the woodland floor, which encourages the growth of woodland herbs and greatly increases the number of species the woodland supports. The other reason appears paradoxical, but is not. Coppicing is exploitive, in that it removes material (wood) without using fertilizers or even compost to restore the nutrients taken from the soil. In time, therefore, the soil is depleted. This inhibits the growth of aggressive plant species that are able to overwhelm others only if they receive ample nutrients, thus allowing a wide variety of less aggressive species to flourish. In the last few years, pro-coppicing conservationists have found new allies, because this management system seems ideally suited for the production of small wood for use as fuel for power stations.

Plantation forestry has proved the most effective way of ensuring a sustained supply of timber and wood products in temperate regions and it is now being introduced in the tropics. Plantation tree species are chosen for their rates of growth and the quality of their wood. In most cases this leads to the selection of species that are not native to the areas where they are grown. In temperate climates these exotic species are conifers and in the tropics they are often eucalypts, cypresses, and pines.

Many tropical plantations have succeeded, but there are difficulties. Not the least of these is the fact that rural communities in the tropics are more highly dependent on products they obtain from the natural forest than are people living in higher latitudes, and plantations may not supply them. Where they do supply them, commercial plantations must charge for materials, such as fuelwood, that formerly were free. Many fuelwood plantations have failed for this reason. Other plantations have failed because trees were planted without testing them in the environment first, and they did not grow well, because no markets could be found for their products, because corruption depleted the resources needed for investment, or because the concept was imposed on people who rejected it rather than being developed with their full cooperation. Nor are plantations the only means available to produce wood on a sustainable basis. With proper management and protection from fire, cleared areas of tropical forest will usually regenerate a natural secondary growth. This may be ecologically inferior to the original primary forest, but its timber is satisfactory (PERSSON, 1995a) for fuel use and many other purposes.

The pressures leading to the clearance of tropical forests are identical to those responsible for the removal of temperate forests. Some combination of natural regeneration and carefully planned plantation may be sufficient to secure a regular supply of timber, in the tropics as in higher latitudes, but we should not look to them to solve wider problems.

In particular, plantation and regeneration forests have little effect on the rate of forest clearance. Forests are cleared, as they have always been, to provide land for agriculture, not because of the demand for forest products. Agricultural land is needed by impoverished people who hope to farm it at a little above subsistence level. That pressure would be reduced by increasing employment and so providing people with an alternative to farming. Their wages would then purchase food grown more

efficiently on a smaller area of land by adequately capitalized methods. Like large-scale agriculture, however, most commercial forestry is highly mechanized and provides little employment.

Sound forest management provides us with forest products on a sustainable basis. The forested area is increasing in many high-latitude countries, including Britain, and may well be increasing overall. If we wish to reduce the rate at which primary tropical forests are being cleared, better forest management will not suffice. Far more radical economic, social, and political reforms will be needed.

54 Farming for food and fibre

Farming began, with the deliberate cultivation of cereals, rather more than 10000 years ago in the Middle East (HARRIS, 1996), possibly at about the same time in Taiwan (BENDER, 1975, p. 223), and perhaps 5000 years ago in Central America (BENDER, 1975, p. 10). The cultivation of non-cereal crops, such as pulses, began at about the same time or soon afterwards. Why farming began is uncertain, but once established it spread through lands between the Tigris and Euphrates Rivers and by about 6000 years ago food productivity had increased sufficiently to support urban populations (BRAIDWOOD, 1960). In the space of 4000 years, the new technology spread throughout western Europe (BENDER, 1975, p. 13). The dog was the first animal to be domesticated, in a process that began at least 12000 years ago, followed by sheep, goats, and pigs rather more than 7000 years ago, and western cattle (descended from *Bos primigenius*, the aurochs) about 1000 years later (CLUTTON-BROCK, 1981, pp. 34, 56, 60, 66, 72).

It was not a sudden transition, with people abruptly changing their way of life as soon as travellers or immigrants explained the new technology to them. Hunters developed a close relationship with and understanding of the animals they hunted. Perhaps they held them in enclosures until, gradually, they were tamed. People who gathered food might observe that spilled seed sprouted and start to scatter it deliberately. As they did so, they would have inadvertently commenced the process of selective breeding. Wild cereals, for example, shed their seeds as soon as they ripen. This makes them difficult to gather and people would probably have selected those individual plants that retained their seeds a little longer, and these would have supplied a higher proportion of the seeds that were sown than they represented in the wild population. Eventually, this led to the immediate ancestors of our modern cereals, from which the seeds must be removed by a separate operation (threshing) after harvest. Other food plants developed from individuals chosen from the wild population because they possessed certain desirable properties, such as size or flavour. In those days neighbouring communities would have met in the course of their hunting and gathering, and interesting information would have travelled quickly.

Crop cultivation encouraged the establishment of settled communities on the better land and this led in turn to emigration and the colonization of adjacent areas. Shifting cultivation will support only a limited number of people, so where it was practised an increase in the population meant some had to leave and start a new community elsewhere. For communities using more efficient farming methods it was probably impracticable to cultivate fields more than about one hour's walk from the village. Again, an increase in population would necessitate emigration (BENDER, 1975, pp. 13–14). Early farmers continued to rely on wild foods for a surprisingly long time. Although they were probably fed ceremonial meals prior to their ritual killing, people whose bodies have been recovered from Danish bogs had eaten a variety of wild grasses and herbs as well as cultivated grains, and those people lived in the Iron Age, Tollund man around the time of Christ and Grauballe man around AD 310±100 years (GLOB, 1969, pp. 33, 57). Since we still rely on hunting as the principal means of obtaining fish, wild birds are still shot and eaten, and in rural areas people continue to collect edible wild fungi and gather blackberries, sloes, and other berries from hedgerows, it appears we have not entirely abandoned the old ways of obtaining food even now.

Those who till the soil require tools. At first these were simple sticks for digging and hoes for removing weeds, but the technology advanced dramatically with the introduction of the plough. Probably invented by the Babylonians, this was used in ancient Egypt (see Figure 5.19A) and the modern plough (Figure 5.19C) is its direct descendant. Drawn by oxen, in some parts of the world to this day, horses or, on modern farms, by a tractor, the plough cuts into the soil, aerating it and



Figure 5.19 Ploughing and sowing. A, Ancient Egyptian plough. B, Babylonian plough and seed drill (c. 1316 BC). C, Modern single-furrow plough

improving its drainage. The principal innovations in modern ploughs are the mouldboard, which turns over the ploughed soil, breaking weeds and burying their foliage, and the coulter. This is a disc (or on some ploughs a knife) that cuts the soil to a predetermined depth ahead of the point and wing of the share. The plough shown cuts a single furrow, but most tractor-drawn ploughs cut several at the same time. As long ago as Babylonian times, ploughing was being combined with sowing by attaching a seed drill, comprising a container into which seed is poured and from which it falls through a hole and down a tube into the ground (see Figure 5.19B). The seed drill did not reach England until Jethro Tull introduced it, amid considerable controversy, in about 1730 (PARTRIDGE, 1973).

Ploughing aerates the soil, stimulating the activities of soil organisms, but by exposing it to wind and rain ploughing also accelerates weathering. This increases the rate of soil formation, but it also leads to erosion. Where rainfall is insufficient for the needs of crop plants, irrigation may be necessary. Supplied carelessly, or in ignorance of the risks, this can lead to salinization, especially in the seasonally dry climates of the Mediterranean, where irrigation is most needed. Environmental problems caused by farming emerged in ancient times with salinization in the Tigris and Euphrates valleys, and the severity of soil erosion in Greece was described by Thucydides (*c*. 465–400 BC) (HYAMS, 1976, pp. 92–94). Today, it is estimated that in the world as a whole about 80 per cent of agricultural soils are to some extent eroded (THOMPSON, 1995). Even in Britain, where the mild, maritime climate favours agriculture and limits soil erosion, most cultivated land near the top of slopes is to some extent eroded.

When soils show signs of failure farmers have two choices. They may extend the area they cultivate into previously uncultivated, 'virgin' land, or they may intensify production on existing land. In practice, they do both.

Intensification is achieved by using fertilizers to augment soil nutrients and pesticides to reduce crop losses, and by breeding new crop varieties and breeds of livestock that respond better to the changed circumstances and consumer demand than the varieties and breeds they replace. This type of intensification began in Europe in the eighteenth century and accelerated greatly in Europe and North America from the 1940s, when governments provided the economic stability that allowed farmers to invest in their farms and systems of grants and subsidies that encouraged them to do so.

A version of this type of intensification was introduced much more rapidly in Latin America and Asia. New varieties of wheat were developed at the Centro Internacional de Mejoramiento de Maíz y Trigo, in Mexico, and at Washington State University in the United States, by a research programme that began in 1943. By 1977 these wheats were growing on 30 million hectares, nearly half the wheat-growing area in developing countries, and yields increased from about 8 tonnes per hectare for traditional varieties to 15–20 tonnes per hectare. Indian wheat production tripled between 1969 and 1979. Research to develop new rice varieties began in the early 1960s at the International Rice Research Institute in the Philippines, and the first of the new rices, IR-8, entered commercial use in 1966. The new rice varieties, of which there are many, are now grown widely in Asia. They grow and ripen more quickly than traditional varieties, so two or even three crops a year can be grown on the same land. Yields have risen from less than 2 to up to 16 tonnes per hectare. This transformation of low-latitude farming was described in the Indicative World Plan for Agricultural Development, a massive document prepared by the Food and Agriculture Organization of the United Nations (FAO). Journalists nicknamed it the 'Green Revolution' (ALLABY, 1977, pp. 101–133). Improvement has occurred more slowly in sub-Saharan Africa, partly because of a lack of new varieties of millets and sorghum, but also because of war and drought.

Dramatic though the results of intensification have been, they have generated problems of their own. Some have been social and economic, where the sudden improvement in the profitability of farms has led landowners to seize all the gains for themselves, leaving tenants no better off than before, or to evict tenants altogether. The provision of credit facilities and efficient infrastructure has often delayed improvements in the more remote areas. The increased use of fertilizers and pesticides has also caused pollution.

Several researchers also pointed out that the operation of farm machines and the production and application of agricultural chemicals consume energy. Since food can also be described in terms of energy they constructed energy budgets suggesting that intensification exacted a price. Averagesized British dairy farms consumed 26.5 GJ ha⁻¹ and yielded 14.6 GJ ha⁻¹, pig and poultry farms consumed 44.8 and yielded 14.1 GJ ha⁻¹, and broiler chicken farms consumed 58.9 and yielded 5.87 GJ ha⁻¹, in each case the energy coming from fossil fuels (LEACH, 1975, pp. 110–111, 125). Parallel studies by William Lockeretz at the Center for the Biology of Natural Systems, Washington University, St Louis, published in 1975, reached similar conclusions in respect of US agriculture. Much was made of these findings at the lime, the 1970s being a period of anxiety regarding the security of oil supplies to the industrialized countries, but it can be argued that it is sensible to use inedible fuels to produce food, provided the agricultural system is not so extreme as to become economically nonsensical. This does not resolve the issue, of course, because even if this is a wise use of fuel, fossil fuels are not inexhaustible and so energy-intensive agricultural systems may prove unsustainable in the long term. Fuel is used in agriculture in the manufacture of tools, machines, and other equipment, to power machines, and in the manufacture of fertilizers and pesticides. It is not inconceivable that alternatives could be substituted for all these uses. Electrical power from nuclear generation, for example, might power factories and drive machines. This consumes no fossil fuel, and the uranium on which it depends, though also non-renewable, is at present abundantly available, and should it become scarce in the future, by that time fission generation may have given way to another means of power production. Hydrogen, ethanol, or methanol might power farm machines. The feedstock chemicals used in fertilizer and pesticide production are widely available naturally; fossil fuels are used to supply them only because at present these provide the cheapest and most convenient source.

Energy budgeting in agriculture

In the 1970s, several academic studies were made comparing the amount of energy used in the production of food for human consumption and the energy value of that food. In Britain, Gerald Leach prepared a report, *Energy and Food Production*, that was published in 1975 by the International Institute for Environment and Development. It was this report which stimulated vigorous debate in Britain, but similar debates took place in the United States and other countries.

Leach collected data for the output of food from British farms. He then made allowances for food lost by wastage after harvest to produce a 'net edible output'. This was converted into energy values using standard conversion figures used in dietetics. He had now produced figures representing the energy content of home-grown food entering the public supply, the output energy.

Input energy took account of all fuel and electricity purchased by food producers and 40 per cent deducted because it was for domestic use. Agricultural chemicals were assessed in terms of the energy per tonne required to produce them. Machinery was assessed by the energy consumed during all the processes leading to their manufacture. In use, it was assessed by the fuel consumed for standard operations, such as ploughing, harrowing, and combining. Foodstuffs for livestock were assessed on the assumption that they had been grown on farms in Britain, or farms indistinguishable from British ones, with similar energy requirements. Transport, services, and the construction of farm buildings were also included, and so was human labour, measured as the food required by the workers.

Finally, the energy required to produce unit amounts of food (the input) was compared with the food energy in the edible product (the output). Leach calculated that the average ratio of energy output: energy input in specialist dairying was 0.38; in cattle and sheep rearing 0.59; in sheep farming 0.25; in pig and poultry farming 0.32; and in cereal-growing 1.9. After processing, the figures were even more startling. White, sliced bread had an energy output: input ratio of 0.525, broiler chicken 0.10, battery eggs 0.14, and winter lettuce grown under glass 0.0017.

Expanding the area of cultivated land is more difficult. Almost all the land suitable for agriculture is being farmed, and although there could be some extension into marginal lands, yields from them are unlikely to be great and might do little more than compensate for yield reductions on degraded land.

As Figure 5.20 shows, the amount of food produced per head of population has remained fairly constant through the 1990s, but its balance is changing. In the developed countries over-production and the desire for wildlife and landscape conservation in rural areas have led to a reduction in food output, but in the less developed countries output continues to increase steadily. Figure 5.21 shows that overall output of cereals has remained generally steady, although there was a drop in output of coarse grains, used to feed livestock, in 1993–94. In *Agriculture: Towards 2010*, a review of world agriculture it published in 1992, the FAO (*www.fao.org/*) showed



Figure 5.20 Indices of per capita food production 1990–94 (1979–81=100)



Figure 5.21 World production of cereals during the 1990s (millions of tonnes)

that over 30 years world food output per person had risen 18 per cent and the number of malnourished people had decreased from nearly 950 million to 800 million in 20 years. It predicted that by 2010 this figure will fall to 650 million. Poverty was the principal reason for hunger, as it has always been. Between 1990–92 and 1995–97 the extent of malnourishment decreased in 37 countries and the number of people going hungry decreased by 40 million. The number of malnourished people remains unacceptably high, estimated at 790 million in 1999, but it is falling in line with the FAO projection.

It is not only food that farmers produce. Fibres, such as cotton, wool, silk, and flax, are also important. Wool is closely linked with meat production, of course, and silk is produced very intensively in indoor units, although land is needed to grow the mulberry and other trees that supply the leaves on which the larvae feed. In 1997, the world produced 52700 tonnes of silk. Cotton and flax, on the other hand, compete directly for land with food crops. Flax is little used nowadays, although interest in it has revived somewhat, but in 1998 world production of cotton amounted to 18.6 million tonnes. Annual world cotton output is slightly lower than that of artificial fibres, which is predicted to continue increasing.

In years to come it is desirable that we improve the nutritional status of the very poor. This implies a continuing increase in food production, although the primary need is for economic advancement in particular countries. The need to grow more food on essentially the same area of land might suggest changes in our land-use priorities, but this is not so simple as it seems. We might argue, for example, that fibre crops, such as cotton, are no longer needed. Synthetic fibres provide adequate substitutes, and abandoning cotton-growing would free land for food production. The same case is sometimes made for cash crops, such as tea, coffee, and tobacco, which are grown for export. Perhaps tobacco-growing will be abandoned one day, but for reasons of public health, not economics. Cash crops, and cotton, allow countries to earn currency with which to build their manufacturing industries. It is difficult to see how they could advance from their present level of economic

development without exporting agricultural produce. Were the tea, coffee, and cotton plantations to close, the land would not necessarily produce food, because unemployed people could not afford to buy it. Hunger would persist.

It is also maintained by some that world food production could increase dramatically were we to abandon, or at any rate drastically curtail, livestock production. This is because pigs and poultry, and to a lesser extent cattle, are fed cereals that could be eaten directly by humans, the animals achieving a maximum of about 10 per cent conversion efficiency. In other words, of the grain they eat, 90 per cent or more is lost in respiration. There is some truth in this, but it is only part of the story. Not all livestock consume grains and large areas of the world are suitable only for the production of pasture. Grass is the only practicable crop over much of Britain, for example, and it is fed to cattle and sheep. Reducing the number of cattle and sheep would not increase the amount of food produced unless people were prepared to accept food made directly from grass. It is technologically possible to convert grass into food suitable for human consumption, but it probably costs more than leaving animals to do it by themselves and consumers might not be prepared to pay more for what appeared to be an inferior substitute. It is not even true that all pigs and poultry eat only grain suitable for human consumption. Most do, in intensive units to produce cheap meat and eggs, but they can also eat spoiled grain and other foods that are not suitable for human consumption and would otherwise be wasted. Indeed, this was their traditional agricultural role.

Many people go hungry in the world, but their number is decreasing. Gains are being made and the agricultural improvements achieved in the last thirty years are truly impressive. With food production, as with so many of the dilemmas facing us, however, the most obvious solutions are often wrong in a situation that is much more complex than it sometimes seems.

55 Human populations and demographic change

When Charles Darwin read a long essay by Thomas Robert Malthus (1766–1834), the first edition of which was published in 1798, he found it provided him with a mechanism to drive natural selection. The struggle for existence, Darwin wrote, was 'the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdoms; for in this case there can be no artificial increase of food, and no prudential restraint from marriage' (DARWIN, 1859, Ch. 3).

Today, there is widespread anxiety about the rate at which the human population of the world is increasing. The fear is not new. The Zoological Society of London was founded, in 1825, partly to identify animals suitable for domestication and acclimatization to new parts of the world, in order to increase the food supply for growing populations (BURGESS, 1967, pp. 87–88). From figures in parish registers, the population of England and Wales is estimated to have been about 5.2 million in 1695 and 9.2 million by 1801. After 1801 the figures are based on census returns. They show that by 1851 the population had risen to 17.9 million and by 1901 to 32.5 million (TRANTER, 1973, pp. 41–42).

It is little wonder that the increase caused alarm and that the increase in world population continues to do so. As the familiar graph in Figure 5.22 illustrates, the rate of increase appears to be exponential. Exponential or geometric growth occurs when the increment accrued during each period is added to the total before the next increment is calculated. It is contrasted with arithmetic growth, in which increments are calculated against the original quantity, accumulated separately, and added to the original quantity at the end. In financial terms, these are known as compound and simple interest respectively.



Figure 5.22 Rate of world population growth

This was the distinction on which Malthus based his argument (MALTHUS, 1798). He pointed out that parents are capable of producing more than the 2 children required to replace them in the population. If, for example, each pair of parents produces 3 children in each generation, and we start with two pairs (to avoid inbreeding!), the number in each generation proceeds as: 4; 6; 9; 13.5; 20.25; 30.375.... Using information from populations in the then sparsely populated United States, he went on to assert that human populations double in size every 25 years (a 2.8 per cent annual rate of increase). If a quantity is increasing exponentially, the time taken for it to double can be calculated approximately by dividing 70 by the percentage rate of increase; if the annual rate of increase is, say, 2.0 per cent, the doubling time will be $70 \div 2=35$ years.

People require resources to sustain them, the most obvious being food, but Malthus asserted that food output can increase only arithmetically.

The population of this island is computed to be about seven millions, and we will suppose the present produce equal to the support of such a number. In the first twenty-five years the population would be fourteen millions, and the food being also doubled, the means of subsistence would be equal to this increase. In the next twenty-five years the population would be twenty-eight millions, and the means of subsistence only equal to the support of twenty-one millions. In the next period, the population would be fifty-six millions, and the means of subsistence just sufficient for half that number (MALTHUS, 1798, pp. 74–75).

In other words, the geometrical rate of population increase inevitably outruns the arithmetic rate at which resource availability can be made to increase. Population is then held in check, through hunger and disease or voluntarily by producing fewer children. This is the 'Malthusian limit' toward which our numbers are said to be heading. All present fears over global population increase derive from this line of argument.

The argument sounds persuasive, but it was not really fear of overpopulation that led Malthus to advance it. He was seeking to refute ideas current among certain intellectuals in the years following the French Revolution, and held by his own father. They believed that new scientific discoveries and radical political and economic change offered the promise of improvements in the living standards of ordinary people that could barely be imagined. Malthus claimed to prove mathematically that 'population must always be kept down to the level of the means of subsistence' (MALTHUS, 1798, p. 61). From this it followed that attempts to improve living standards, by increasing the availability of resources, must lead to a population increase sufficient to consume the additional resources. This would leave people worse off than before, because a greater number of them would be living in want. The kindest strategy was to treat the poor harshly and on no account seek to alleviate their lot. The Malthusian argument was used to defeat a campaign to institute a minimum wage and led many politicians to believe that relief for the poor simply produced more wretchedness. In particular, Malthus urged in the succeeding years, no allowances should be paid for children (ALLABY, 1955, pp. 163–166).

By 'proving' that poverty can never be eliminated, the Malthusian characterization of human demography places responsibility for their plight firmly in the hands of the poor. If they wish to prosper, they must reduce their number. Should they fail to do so they will have only themselves to blame when their children starve, as assuredly they will. Malthus regarded the poor as feckless. Had he not done so, he might have observed that according to his argument the rich, with ample access to resources, should multiply until they exhausted those resources and reduced themselves to poverty. On the contrary, however, they tended to have fewer children than poor people. Malthusianism regards poverty as the fault of the poor, whose ignorance of their own best interest will defeat any attempt by the rich to help them.

Contemporary 'neo-Malthusians' accept the Malthusian premise, but moderate it by advocating programmes for population control, mainly through the provision of contraceptive devices and information. They also point to the disproportionate allocation of material resources to the wealthy: the European and North American standards of living are sustained by vastly greater consumption of resources than are available to the citizens of poor countries, and Western economies appear to grow mainly by artificially stimulating consumption. A more equitable distribution of access to resources would, in their view, increase the likelihood that the great majority of the world's people might live in decency, their essential needs met. Anti-Malthusians reject this line of reasoning. They maintain that rather than there being a kind of levelling down, which in any case would be politically and probably economically impossible, poor countries should be helped to expand their economies and, by implication, their levels of resource use. This, they believe, would improve living standards directly and reduce rates of population growth indirectly, and the availability of resources would increase as demand required. Resources, according to this line of reasoning, should not be regarded as 'renewable' or 'non-renewable', so much as flexible, with virtually unlimited capacity for the substitution of one that is abundant for another that is less so.

In the event, Malthus was wrong. Advances in agricultural methods increased output to a far greater extent than he imagined possible and living standards improved greatly. Today, with a population of 58 million, the British people enjoy much better nutrition than they did when there were only the 7 million of them he described. In 1791, the population of England and Wales was increasing annually

at about 1.0 per cent (TRANTER, 1973, p. 41), not the 2.8 per cent on which he based his calculations, and as prosperity increased during the nineteenth century the rate of increase never exceeded 1.8 per cent (between 1811 and 1821). For most of this century it has remained below 1.0 per cent and at present it is below 0.7 per cent. At the time Malthus wrote his essay, no country had experienced the 'demographic transition'. This is the process by which death rates fall in a previously stable population, but birth rates remain unchanged. This generates an increase in the population. Eventually, birth rates also fall, until birth and death rates balance once more and numbers stabilize.

In the world as a whole, however, population is certainly increasing rapidly. As Figure 5.23 shows, it has risen from around 1 billion in 1850 to 5.6 billion in 1994, and the United Nations officially designated October 16, 1999, as the date of birth of the world's six-billionth citizen. According to the United Nations median estimate, it is likely to reach 8.25 billion by 2025. Steep though the increase is, the curve in Figure 5.23 is less dramatic than that in Figure 5.22. It is also more credible, because only the crudest guess can be made of the size of the world population many centuries ago.

Exponential growth appears on a graph as a curve that rises at a very shallow angle for a long time, then suddenly turns upward until it rises almost vertically. The curve in Figure 5.22 is exponential and that in Figure 5.23 might be, but in this case it is less certainly so. Biological populations sometimes increase exponentially, in a J-shaped curve, then collapse. That is what some people fear may befall the human population. More commonly, though, their growth follows an S-shaped



Figure 5.23 World population (billions) 1850–2025 (median estimate)

curve, rising rapidly for a time, but then stabilizing owing to density-dependent factors. The curve in Figure 5.23 could develop into an S-shaped curve.

There is good reason to suppose this is what is happening. When fears of a 'population explosion' were popularized in the late 1960s, the rate of increase was about 2.0 per cent, doubling the world population every 35 years. More recently, as Figure 5.24 illustrates, it has been falling. The fall has been erratic, but the trend is clearly downward. Between 1997 and 1998 it fell from 1.47 per cent to 1.42 per cent (HAUB, 1999). Some forecasts predict a decline in the world population, starting in about 2050.

Population growth is confined, almost entirely, to the less industrialized countries—in other words, to the poor. This may seem to support the Malthusian model, but it is equally characteristic of a demographic transition. Improved health services and nutrition led to a reduction in perinatal, infant, and childhood mortality. Death rates fell, but the same number of babies continued to be born. That is why the population increased so sharply. If health improvements are sustained, parents come to accept that fewer babies need be born to provide the number of offspring needed to help with the work and care for them in their old age. If education is then made compulsory for all children, child labour is reduced. Children cease to be productive workers and become economic dependants, reducing further the incentive to have large families. The most important reform then is to improve educational opportunities for girls and employment opportunities for women. This allows women the choice either to stay at home bringing up a large family, or to work outside the home and contribute directly to the household budget while enjoying the social life and prestige paid employment brings. Hardly surprisingly, this is what many women choose. Provided adequate contraceptive advice and materials are easily obtainable, birth rates then start to fall.

This is the demographic transition. Many countries have implemented the necessary reforms, and the total fertility rate (the number of children a woman will bear during the course of her reproductive life) is falling. In the 1950s, the world average fertility was 5 children. By the late 1990s it had fallen to 2.7, and the annual increase in population had fallen to 78 million, from 90 million in the 1980s. In 1999, the fertility rate in 61 countries was below the 2.1 needed to maintain



Figure 5.24 Estimates of the rate of global population increase since 1975 (%)

a constant population size. In most of Europe, the Caribbean countries, and eastern Asia including China, populations are set to decrease and in others it will increase, but only slowly. In Thailand, for example, the fertility rate fell to 2.3 from 6.4 in 1960. Since the 1980s it has fallen in Ghana from 6.0 to 5.4 and in Kenya from 8.0 to 5.4. (HAUB, 1995). This change is happening everywhere, even in the poorest countries. The fertility rate in Bangladesh has fallen from 6.2 to 3.4 children in ten years. There are 18 countries in which the population may decrease by 15 per cent by 2050. In Bulgaria, for example, the 1999 population is 8.3 million and its predicted 2050 population has been revised from 7.8 million to 6.7 million (PEARCE, 1999).

It appears that the rate of population increase peaked in the 1960s. The 1999 UN medium population projection for 2050 has been reduced from 9.4 billion to 8.9 billion, but some demographers believe this is too high. They calculate that the world population will peak at about 7.7 billion in 2040 and then enter a long decline leading to a population of less than 6 billion by 2100 and about 3.6 billion by 2150 (PEARCE, 1999).

There is inevitably a delay in any such transition. While the birth rate exceeds the death rate, causing a population to grow, it is children who are being added and consequently the average age of the population decreases. As the children enter the reproductive stage of their lives their children will cause the population to continue growing. More parents imply more children, even if the new parents have fewer children than did their own parents. Signs that this phase of the change is ending appear as a reduction in the number of children. In 1990 there were 623 million children in the world below the age of five. In 1995 this figure was 614 million. The change had begun, but the world population will continue to increase for some time—at least until about the middle of the next century. For the same reason, when the increase ends the resultant population will be much larger than it was before the increase began. The British population is no longer growing, but it has increased from 7 to 58 million. As populations decrease, nationally and globally, the average age of the population increases. This can impose burdens on societies caring for people who are too old to be economically active.

A rapid increase in population also places a heavy burden on financial resources, because the economically active members of the population must support a larger number of dependants. This leaves less money for investment in productive industries and thus inhibits the economic development needed to sustain the reforms that will reduce the rate of growth..

Increasing prosperity will lead to a much increased demand for material resources. The challenge of the coming decades will be to supply them without imposing too heavy a burden on the natural environment. Environmentally, we have no alternative. Land is degraded primarily by the very poor seeking to scratch a living from it in ways that deplete it. Industrial pollution is much greater from factories equipped with obsolete plant whose managers must cut corners if they are to compete with more modern plants overseas. Even pollution by transport is reduced if the vehicles are new and incorporate modern devices to improve fuel efficiency and minimize emissions. The industrialization of the presently less industrialized countries may cause environmental problems, but a lack of industrialization and consequent poverty will not lead to a more wholesome environment.

56 Genetic engineering

Organic farmers are familiar with *Bacillus thuringiensis*. They have been using it for many years as a kind of living insecticide. It was first identified in 1911; cultures were being sold commercially in France in 1938 and it was used to control Japanese beetle in the United States in 1939 (GOLDSTEIN, 1978, p. 173). *Bacillus thuringiensis* kills leaf-eating caterpillars. It does so by producing a protein

that turns into a lethal poison when the insect ingests it. Different strains of *B. thuringiensis* produce toxins effective against different insects, so farmers often spray a mixture of strains.

Even with a substance as environmentally safe as *B. thuringiensis*, however, spraying is a crude and wasteful way to deal with pests. It would be much better if the plants produced the active ingredient themselves. No pest could then escape the poison, because every leaf would be poisonous, and the grower would not have to invest in spraying equipment and wait for suitable weather conditions before using it. In the case of *B. thuringiensis* this is possible, because the poison is a naturally produced protein, encoded genetically. Identify the relevant bacterial gene, remove it, insert it into the plant cell nucleus, and all being well the plant will now produce the protein. It is nowhere near so simple as this makes it sound, but scientists have mastered the necessary techniques and the *B. thuringiensis* gene has been or is in the process of being introduced into varieties of a number of crop plants. Tobacco was the first to receive it, in 1987 (VAECK *ET AL.*, 1987), followed by rice in 1993, potatoes in 1995, and then tomatoes, cotton, maize, and sunflower. This is genetic manipulation, popularly known as 'genetic engineering', the deliberate alteration of organisms by the introduction of genetic material previously alien to them. The technology promises to make agriculture much more sustainable (PLUCKNETT AND WINKELMANN, 1995).

DNA (deoxyribonucleic acid), the compound comprising the material of heredity, consists of four bases, or nucleotides: the purines adenine (A) and guanine (G), and the pyrimidines thymine (T) and cytosine (C). These are linked to form two chains wound helically; A can pair only with T, and C with G. The bases work in threes, called codons or triplets, each codon specifying a particular amino acid. A gene consists of a sequence of codons, with particular codons marking the start and end of the sequence. It is rather like a sentence written using only these four letters, but beginning with a capital letter and ending with a full stop. A functional gene (many genes have no apparent function) encodes all the amino acids required to construct a particular protein. In addition to the proteins from which muscle and tendon are made, enzymes and antibodies are also proteins. Since protein molecules vary greatly in the number of amino acid molecules they contain, genes also vary in size. In plants and animals, the genetic code is contained in the cell nuclei (although certain cell organelles have DNA of their own). In prokaryotes, such as bacteria, there is no nucleus and the DNA is carried 'free' in a single chromosome. Bacteria also contain plasmids, loops of DNA that pass readily from one cell to another.

Once the gene encoding a desired protein has been identified it can be excised from its long DNA strand by means of restriction enzymes. These evolved in bacteria as a defence against viral attack, which they restrict (hence their name) by severing DNA at certain nucleotide sequences, each restriction enzyme attacking particular sequences. When some restriction enzymes cut DNA they leave two nucleotides from one DNA strand protruding beyond the end of the other strand. This is known as a 'sticky end', because these protruding nucleotides will anneal to a complementary pair protruding from another DNA strand. If AC protrudes, for example, a strand with protruding TG will bond to it and this will happen even if the DNA comes from quite unrelated organisms. This allows excised segments of DNA to be recombined in new ways, as recombinant DNA, with the help of a ligase, another enzyme that strengthens the bonds by which the segments are annealed.

Use a restriction enzyme to break open a plasmid, leaving appropriate sticky ends, add a gene, with complementary sticky ends, excised from another organism, and the excised gene will be inserted into the plasmid, the ends of which will rejoin to form a closed loop. The plasmid then contains all its original genes, plus the introduced gene. Because plasmids readily cross bacterial cell walls, the altered plasmid can be introduced into bacteria. These can then be cultured, the plasmids replicating as the cells themselves replicate, and the bacteria containing the modified

DNA injected into another organism. Figure 5.25 illustrates the process. The introduced gene may be a replacement for a defective gene in the host. This is the basis for gene therapy. If it is a gene alien to the host, the host is called 'transgenic', because it carries one or more genes from a different species (TUDGE, 1993, pp. 206–214).

Plasmids are commonly used as vectors, the means by which genes are transported into a host, but there are others. Deactivated viruses and 'naked' DNA are sometimes used. They are also cloning vectors, producing an identical copy, or clone, of the desired gene each time they replicate, but genes can now be replicated by themselves before being introduced into a vector.

This is made possible by the polymerase chain reaction (PCR), the invention for which Kary B. Mullis won the 1993 Nobel Prize for Chemistry. DNA is added to a solution containing 'primers', one of several possible DNA polymerase enzymes, and rich in purines and pyrimidines. The solution is warmed to 95°C, at which temperature the two DNA strands separate. It is then cooled to about 50°C and the primers anneal one to each end of the separated strands. It is warmed to about 70°C, and the polymerase builds a complementary DNA strand to each separate strand, forming double strands. At each repetition of the process the amount of DNA is doubled.



Figure 5.25 One method of genetic engineering

Despite all that has been written in the press about gene therapy for humans, installing functioning genes in human bodies has proved difficult and so far the successes are modest (MARSHALL, 1995), although there is good reason to hope that eventually gene therapy will bring significant benefits (CRYSTAL, 1995). In plants, on the other hand, there has been much greater success, especially in conferring resistance to pests and diseases.

This is not really new. Plant breeders observed in the first years of this century that disease resistance is heritable in a Mendelian fashion and can be bred into commercial varieties. Today the genetic details of such resistance have been discovered and appropriate genes can be introduced into plants that can benefit from them (STASKAWICZ *ET AL.*, 1995).

GM Foods

On August 10, 1998, Arpad Pusztai, a specialist in lectins working at the Rowett Research Institute, near Aberdeen, said in a TV interview in World in Action that his research had found that potatoes, genetically modified to contain a gene for the production of a lectin found in snowdrops, had stunted the growth of rats fed on them. This claim led to his suspension, and later to his retirement (he was well past retirement age), because his work had not been published and there was doubt over his interpretation of its results. On February 12, 1999, British newspapers reported that scientists from 13 countries had backed Pusztai's findings and were calling for his reinstatement. The scientists were revealed as friends and colleagues of Pusztai, some with known anti-GM views, but it was too late and the issue developed into a major food scare. Greenpeace and the Soil Association called for an outright ban on genetically modified (GM) foods and as sensational, antiscientific press stories, based on misinformation from environmentalist groups, increased public alarm, the environmentalists were able to claim to represent public opinion. Environmental activists destroyed GM crops being grown under test conditions to determine their effect on the surrounding environment.

A team of scientists from the Royal Society examined the Pusztai experiments and concluded his study was flawed in its design, execution, and analysis. Eventually, the Pusztai paper was published in *The Lancet*, despite strong scientific opposition (LODER, 1999). The effect of the anti-GM campaign was to remove all GM foods and foods containing GM ingredients from British shops. Millions of people, in several countries, had been consuming GM foods for a number of years and no evidence whatever had emerged that GM foods were harmful to health or to the environment.

In 1999 it was estimated that in the world as a whole GM crops were being grown on almost 40 million hectares. This was an increase of 44 per cent over the area growing GM crops in 1998 and occurred mainly in China. Argentina, Canada, and South Africa.

Is it safe to grow such genetically engineered plants? Scrupulous tests are conducted before a licence is granted to release any genetically manipulated organism into the environment. In the case of disease resistance, there is no risk to other species. The resistance genes that allow plants to destroy invading pathogens (disease-causing organisms) have no effect other than this and are highly specific In the case of transgenic plants carrying *B. thuringiensis* genes there is the possibility that pests might acquire resistance to the toxin. They have not done so to toxin delivered by conventional application, probably because the toxin breaks down so rapidly that insects are not exposed to it for long enough for resistance to emerge. If entire plants produce the toxin insects may be exposed to it for much longer. So far, however, there has been no sign of pest resistance.

The most widespread application of genetic manipulation has been to introduce resistance to herbicides, and especially to glyphosate, a compound marketed as Roundup. Non-GM crops of maize and soybeans must be sown into ground that has been treated with herbicide to kill emerging weeds. Herbicide treatments must then be repeated several times during the growing season, using sprays that are relatively inefficient because they must not harm the crop. GM crops can be sown without prior spraying and herbicide can be used, without risk to the crop, when the weeds have emerged and are at their most vulnerable. The result is that much less herbicide is needed. Weed control improves, less tillage is required, and soil erosion is reduced. In the United States in 1999 herbicide-resistant soybeans were being grown on about 14 million hectares (ABELSON AND HINES, 1999).

Many aspects of plant growth, including flowering and fruit ripening, are regulated by ethylene (C_2H_4) , a plant growth substance ('hormone') they synthesize and secrete. Certain of the genes involved in ethylene synthesis and recognition have been identified and they may be manipulated to modify ethylene-induced effects (ECKER, 1995). There is also research directed at introducing into crop plants the genes carried by *Rhizobium* bacteria that allow them to fix atmospheric nitrogen, with huge potential for reducing the demand for inorganic nitrogen fertilizer.

The first phase of GM crop plants have been designed to cope better with pests, weeds, and diseases, so farmers are the principal beneficiaries of their introduction. The benefits are not confined to farmers in the industrialized countries. The introduction of disease resistance in bananas, potatoes, and cassava (MOFFAT, 1999) will improve yields in tropical countries. Already, though, crops are being modified to improve their nutritional qualities (DELLAPENNA, 1999), in a second phase that will bring immediate benefits to consumers.

Bacterial cultures, animals, and plants, are also used to synthesize useful substances. Researchers are seeking to develop edible plants that have been genetically manipulated to produce vaccines, for example (MOFFAT, 1995). People eating the appropriate plants would be vaccinated automatically against a whole range of diseases. At first the plants would not be among those forming part of the ordinary diet, so they would have to be eaten specially, like the plants used in herbal medicine, but eventually some dietary plants might also deliver vaccines. Plants are also being modified to produce useful industrial materials, such as cotton plants that yield a polyester-like fibre and rapeseed plants that produce several industrial chemicals. Both plants and bacterial cultures are being used to remove chemical pollutants and others are being genetically manipulated to make them do so. Plants are being modified to tolerate soils contaminated with heavy metals. This will allow crops to be grown on land that until now has been agriculturally useless. The metals would accumulate in the plants, from which those of commercial value could be extracted. Plants storing unwanted metals would be incinerated. In time the land would be cleansed of the contaminants much more cheaply than the usual alternative, which is to remove the soil to a landfill site that can accept hazardous waste (MOFFAT, 1999a).

The environmental implications of these developments are generally benign. Clearly, reducing the susceptibility of crop plants to pests and fungal diseases suggests they can be grown with pesticide applications much reduced or, perhaps, eliminated entirely. This would be environmentally beneficial, because accidents can happen even when safe pesticides are used. If crop plants are rendered resistant

to herbicides, it will be possible to use herbicides in circumstances where they cannot be used at present. Used, as the herbicides would be, among growing crop plants, this is unlikely to cause environmental harm and if it increased crop yields, in principle land might be released for other uses, such as conservation. Wildlife is already returning to American farms growing GM crops. Field trials of herbicide-tolerant sugar beet conducted in Britain in 1998 found herbicide applications were reduced to two sprayings with glyphosate (Roundup), from the customary 5 to 7, using up to nine different compounds. The GM crop attracted more insects than adjacent plots growing non-GM sugar beet, conserved water better, and reduced soil erosion (WILSON *ET AL.*, 1999).

There is no reason to suppose genetically manipulated plants will be unwholesome. They are developed to be eaten, after all and, despite its 'high-tech' image, genetic manipulation is as old as agriculture itself. Few, if any, of the plant and animal products we eat are genetically identical to their wild ancestors. They were selectively bred, and selective breeding is a form of genetic manipulation. Indeed, the concern of some conservationists to maintain populations of animal breeds and crop plant varieties that have fallen from popularity centres on the genetic difference between them and their more commercially profitable rivals.

For some people, ethical issues emerge with transgenic breeds and varieties. Vegetarians and vegans may object to plants carrying genes derived from animals, and the presence of genes derived from pigs or cattle may offend others on religious grounds (ALLABY, 1995, pp. 224–227).

Ethylene and genetic engineering

Ethylene (C_2H_4) is chemically the simplest of all plant growth regulators. It is involved in many processes linked to growth, ripening, and response to stress. Studies of *Arabidopsis* plants have identified the genes producing the proteins that sense and respond to ethylene. This makes it potentially possible to genetically modify a wide range of plants in order to control such matters as growth, root production and pattern, and the ripening of fruit.

Within the next few years it will also become possible to genetically modify plants grown for their oils. By introducing genes identified in non-cultivated species and inserting them into cultivated plants, it will become possible to regulate the types of oil each crop variety produces. The proportion of saturated fatty acids can be reduced, for example, in oils intended for human consumption, and oils with valuable industrial uses can be produced. These developments far exceed what would be possible by conventional plant breeding.

Ornamental plants will also change. Flower colour is genetically controlled. Entirely new colours can be generated as well as plants that grow flowers of different colours side by side.

There is a risk, but it is economic rather than environmental. This is that particular transgenics, especially plant varieties, might be grown on so large a scale as to constitute genetic monocultures over wide areas. Imagine, for example, that a bread wheat was developed that could fix its own nitrogen and thus required no nitrogen fertilizer. Growing costs would be substantially reduced, as a consequence of which wheat prices might fall, and older varieties would become uneconomic and disappear. An attack by a pathogen to which they were not resistant might then prove catastrophic.

This is not fanciful. In 1970, southern corn leaf blight, caused by a newly emerged strain of the fungus *Helminthosporium maydis*, attacked the American maize crop, a substantial part of which consisted of varieties sharing identical cell cytoplasm, which is where the fungus struck. The epidemic was contained, with difficulty and helped by a change in the weather, but not before around 15 per cent of the crop was lost. That episode led scientists to examine the genetic vulnerability of a range of important crop plants (NATIONAL ACADEMY OF SCIENCES, 1972). Increasing that vulnerability would clearly be unwise.

The use of organisms, genetically manipulated or not, to remove pollutants is of obvious environmental benefit, provided its success is not construed as a licence to release pollutants where this could be avoided. (Examples of the use of bacteria in cleaning up oil spills are given in section 61, headed 'Pollution control'.) Similarly, the use of genetically manipulated organisms as sources of industrial chemicals and other products may reduce environmental damage compared with that associated with more traditional production methods.

A risk remains, however, that essentially novel organisms resulting from genetic manipulation may establish themselves in the wild with consequences that were not predicted during their development. The case is cited of calicivirus, imported by Australia from Eastern Europe to discover how effective it might be in killing rabbits. It was planned to investigate this experimentally on Wardang Island, off South Australia, and if it proved successful to release it on the mainland in the late summer or early winter of 1997 or 1998. In October 1995, however, the virus escaped, possibly in insects carried by a mass of cold air, and killed large numbers of wild rabbits on the mainland. If this can happen, might it not also happen with a genetically novel organism?

So far at least, it has not happened, and present indications are that such organisms, modified for human purposes rather than for their own evolutionary advantage, do not compete well with others. Nevertheless, were such an organism to become well established it might persist for a very long time, and the ecological havoc that has been wrought by some introduced species does not fill ecologists with great confidence. Genetic modification is permanent, because it is transmitted from one generation to the next. It is for this reason that all such releases must comply with strict safety rules.

Genetic 'engineering' will bring many changes to our lives in the next few years. Many of these changes will be environmentally beneficial.

End of chapter summary

Like all other animals we use the environment, adapting it to our own purposes, and that environment includes other organisms. If we are to exploit our environment successfully we need to know how species come into being. The principal mechanism for this is natural selection and it is one we have utilized since our ancestors first began farming. Farmers have always selected plants and animals for the traits that make them desirable and this has altered the species genetically. Evolutionary processes also determine the effects of selection pressures introduced by human activities, sometimes inadvertently. The resistance of insects and plants to pesticides and of bacteria to antibiotics is an entirely natural response to selection pressure.

Genetic engineering, or the use of modern, science-based techniques to introduce desired characteristics into species has outraged some environmental groups and they have used their essentially ideological opposition to generate concern among an otherwise uninformed public. Since this has been inflated into an issue of international proportions it is important to understand what the techniques involve and the purposes for which they are used.

Applying the concepts derived from ecology, it is possible to estimate the way our behaviour affects natural ecosystems such as forests and natural populations such as fish stocks. The same concepts also allow us to understand the way our artificial agricultural and urban ecosystems function.

Much concern has been expressed over the last thirty years about the rate of human population growth. This, too, can be understood, at least up to a point, in ecological terms. These propose reasons for human population growth and suggest that it should stabilize naturally. This is what is now happening.

End of chapter points for discussion

How should sea fisheries be regulated? What are the likely consequences of the campaign against genetically modified foods? What is 'biodiversity'? How can we best increase food availability in the less developed countries of Africa, Asia, and Latin America?

See also

Ocean circulation (section 16) Irrigation, waterlogging, salinization (section 25) Erosion (section 29) Wildlife species and habitats (section 49) Biodiversity (section 50) Fisheries (section 51) Forests (section 52) Restoration ecology (section 59

Further reading

- *The Engineer in the Garden.* Colin Tudge. 1993. Jonathan Cape, London. A simple and entertaining account of genetic engineering and the possibilities it offers.
- An Essay on the Principle of Population as it Affects the Future Improvement of Society. Thomas Robert Malthus. First published in 1798, the book is still in print, published by Penguin. There is so much talk about Malthus that it is useful to find out what he actually wrote.
- *Extinction Rates.* Edited by John H.Lawton and Robert E.May. 1995. Oxford University Press, Oxford. An authoritative but somewhat technical account of the most recent thinking on biodiversity and the loss of species.
- An Introduction to Evolutionary Ecology. Andrew Cockburn. 1991. Blackwell Scientific Publications, Oxford. A clear and straightforward explanation of its subject and not so technical as to be inaccessible to those with only a rudimentary knowledge of genetics.
- *On the Origin of Species by Means of Natural Selection.* Charles Darwin. First published in 1859, the book is still in print. Reading what Darwin actually wrote is by far the best way to approach his work, and his writing is very easy to follow.
- *The Problems of Evolution.* Mark Ridley. 1985. Oxford University Press, Oxford (paperback). A clear explanation of evolutionary theory and some difficulties associated with it.
- Soil and Civilization. Edward Hyams. 1976. John Murray, London. A classic on soil, its treatment, and the problems arising from its erosion.

Notes

1 The scaling effect occurs because area is calculated by squaring a value and volume by cubing it. A sphere with a diameter of 4 has a surface area $(4\pi r^2)$ 50.26 and a volume $(4/3\pi r^3)$ of 33.51, a volume: area ratio

of 1:1.50. If the diameter is 6, the surface area is 113.10 and the volume is also 113.10, so the ratio is 1:1. The larger the sphere, the smaller is its surface area in relation to its volume.

2 Figures are from *Britannica Book of the Year 1998*, published by Encyclopedia Britannica, Chicago, p. 129. Although they refer to 1995, the list of the top 20 species changes little from year to year. In 1995, the total world catch for all 20 species was 42682002 tonnes.

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6 Environmental Management

When you have read this chapter you will have been introduced to:

- wildlife conservation
- the history of zoos, nature reserves, and the idea of wilderness, and controversies surrounding them
- pest control
- restoration ecology
- world conservation strategies
- pollution control
- transnational pollution

57 Wildlife conservation

Consider a population of a certain species that occupies a particular range. The population is distributed fairly evenly throughout the range and utilizes the whole of it. Then something happens to fragment the range. Perhaps a network of roads is made through it, or parts of it are ploughed for agriculture or afforested, or rivers intersecting the range become so polluted that individuals drinking from them or trying to swim across them are killed. Whatever the cause, and human activities of one kind or another are nowadays the most frequent, the effect is to divide the population into several groups. These are isolated from one another by barriers they cannot cross.

They cannot cross them, but other things can. Suppose, after a year or two, there is a drought or an unusually severe winter, or perhaps a disease transmitted by insects, or some other chance occurrence that affects all the separate groups and kills many individuals. The population is now much more severely fragmented, its groups very isolated, and each of them may comprise too few individuals to constitute a viable breeding population. Such a sequence of events, illustrated schematically in Figure 6.1, is quite common and leads to the extinction of that species within



Figure 6.1 Effects on a population of fragmentation of habitat

that range. It explains why conservationists place so much emphasis on the need to preserve habitats as the best means to ensure the survival of species.

Loss or fragmentation of habitat is a common reason for extinction, but traditionally conservation efforts have been directed toward species. It is species that are considered to be endangered, rather than habitats. This is reflected in the Red Data Books, started in the 1960s by the International Union for Conservation, Nature and Natural Resources (IUCN also known as the World Conservation Union) (*www.iucn.org/icon_index.en.html*), and the World Conservation Monitoring Centre (WCMC), which introduced what is still one of the principal schemes for classifying 'rarity', the other being the Endangered Species Act 1973, in the United States. The IUCN classification, which is currently being revised, categorizes species by the degree of threat facing them. Categories include 'possibly extinct', 'endangered' for those likely to become extinct if present threats continue, 'vulnerable' for those likely to become endangered if present threats continue, 'rare' for those that are uncommon but not necessarily at risk, 'no longer threatened' for those from which threats have receded, and 'status unknown'.

The scheme has succeeded admirably in drawing attention to the species it lists, but on other grounds it is hardly satisfactory. It is biased heavily toward the better-known species, and new species are added as field biologists report them, rather than on the basis of comprehensive reviews. Only birds have been studied fully. For the remainder, the status of about half of all mammal species has been considered, probably less than 20 per cent of reptiles, 10 per cent of amphibians, 5 per cent of fish, and still fewer of invertebrates (MACE, 1995). As an alternative, it has been suggested that all species be regarded as endangered in the absence of clear evidence to the contrary, but such a scheme would not avoid the need for much more detailed information regarding the less familiar species that limits the value of the Red Data Book (*www.wcmc.org.uk/data/database/rl_anml_combo.html*) approach. Nor do the Red Data Book or Endangered Species Act propose any time-scale for the threats they list, a vagueness that leaves them open to varying interpretations.

Perhaps it is a mistake to concentrate on species, a concept that may be at once too precise and too imprecise to be helpful. Its excessive precision makes it unworkable, because biologists know far too little about most species to be able to apply it in sensible conservation programmes. They opt instead for the conservation of the habitats in which particular species occur. This is a more practicable approach, although one not immune from controversy.

The imprecision of the species concept is revealed at the genetic level. Advances in genetics have led to the concept of the gene pool, which is defined as the complete assemblage of genetic information possessed by all the reproducing members of a population of sexually reproducing organisms. Many conservation biologists now maintain that it is gene pools which should be conserved, rather than species.

In most cases it is not too difficult to decide what constitutes a species (but see section 50, on Biodiversity). Humans are sufficiently different from all other animals to be classified as a species, for example, as are house mice, blackbirds, red admiral butterflies, seven-spot ladybirds, and countless more. Genetically, it is more complicated, and a species is defined by a supposedly typical representative. We are told, for example, that the genetic difference between an average human and an average chimpanzee is smaller than the difference between two humans at the extreme limits of human variability. Humans and chimpanzees differ in less than 1 per cent of their genetic material (in fact about 0.6 per cent), a genetic distance that places them well within the range of sibling species. Taxonomically, there is a strong argument for placing both species within the same genus (PATTERSON, 1978, p. 173). Were humans in need of conservation, we would need to decide whether the preservation of, say, the population of Cumbria, England, would meet the case. Yet

Cumbrians are not genetically identical to Devonians, let alone to the inhabitants of more distant parts of the world, although humans comprise only one species. The species, then, is a convenient but rather crude categorization.

Figure 6.1 shows how the fragmentation of a range may leave a population as small, isolated groups that are no longer reproductively viable. Figure 6.2 shows the possible consequences of such fragmentation on the gene pool. The diagram shows a habitat shared among three species. Members of these species intermingle to a limited extent by moving from one part of the habitat to another. Species 1 and 2 each consist of three populations, and species 3 of four populations. Populations of a species can interbreed, but they are not genetically identical, so there is much more movement among populations (shown only for species 1). The populations of species 2 and 3 occupy areas that meet (b and c of species 2), overlap, or are contained one within another (a and c of species 3). Situations like this are not unusual, especially among marine species, and raise the question of just what it is that species conservation aims to conserve. It is an acute problem with whale conservation (DIZON *ET AL.*, 1992).



Figure 6.2 Population structure for three species within a habitat

Suppose habitat fragmentation destroyed part of the area occupied by one of these species in a way that isolates one or two of the populations. This will produce several gene pools that are impoverished in respect of the total gene pool for all populations. Within each of these gene pools there will be recessive alleles, some of them deleterious. While individuals could mate with members of other populations, most offspring were heterozygous for those genes, so the advantageous dominant allele was the one expressed. In the depleted gene pool, however, recessive alleles have a greater chance of meeting and, of course, they will be expressed in offspring homozygous for those genes. This is the most likely cause of inbreeding depression, and over several generations it reduces population must be to avoid inbreeding depression, but there can be no doubt that provided threats are removed, if the population is genetically healthy its numbers will regulate themselves and it will be safe.

Faced with the risk of inbreeding depression, it is tempting to introduce individuals of the same species from another region, perhaps from another part of the world entirely. This raises a new risk, albeit a less common one, of excessive outbreeding. Some years ago, individuals belonging to two Middle Eastern subspecies of ibexes (*Capra ibex aegagarus* and *C. i. nubiana*) were released in what is now Slovakia in the hope of invigorating the Tatra mountain ibex (*C. ibex*), which had been hunted to extinction but reintroduced from Austria. The subspecies interbred successfully enough, producing fertile hybrids, but whereas the native ibex mated in winter, giving birth to young when food was abundant, the hybrids mated in autumn. The young were born in winter, died, and the population became extinct (COCKBURN, 1991, p. 297).

Despite the risks, species can sometimes be rescued from the very brink of extinction, provided the causes of their decline are clearly identified. The North American bison, or buffalo (*Bison bison*), is a well-known example. With a range that once extended from northern Canada to Mexico and an estimated population of 75 million, by 1883 commercial hunting for meat and hides had reduced the species to about 10000 individuals. From this low level the breeding of captive animals increased numbers. Some are in private herds and others have been reintroduced, as half-wild animals, to the National Bison Range in Montana and elsewhere (BREWER, 1988, pp. 605–606). Similar programmes have also saved the European bison, or wisent (*Bison bonasus*), herds of which now live in various parks and wild in the Bialowieska Forest, Poland (NOWICKI, 1992, pp. 10–11).

Most of the arguments in favour of wildlife conservation are economic, as they have always been. It may be that among the species of which at present we know little there are some that may one day be domesticated for food or other commodities, or yield pharmaceutical or other valuable products. We should not deny our descendants the right to choose whether such species should be exploited. This is an apparently objective argument, but one that is likely to carry little weight with economists, who generally disapprove of investments based on nothing more substantial than the hope that benefits may accrue at some time in the future to people who are not yet even born.

Others offer an aesthetic argument. The world would be a poorer place without the pleasures of watching birds and butterflies, the sight of a meadow ablaze with flowers, the sound of birdsong. Arguments along these lines sound weak, but in fact are strong, because most of us sympathize with them. Unfortunately, however, they begin to weaken as the defence moves away from the most popular species. It can be argued that the world would be a poorer place without slugs, malarial mosquitoes, and the HIV virus. Indeed, the argument is the same, but people may take a little more persuading of its validity.

Still other people maintain that all species have a right to live. It is an opinion which is held strongly, but it raises considerable philosophical difficulties. Do species 'live' at all, or is it individuals that

live? If it is individuals, what precisely do we mean by a right to live, since all individuals must die? Is it possible to confer rights without also imposing obligations which, in this case, conflict with them? If all animals have a right to live, should not the lioness respect the rights of the gazelle?

Some environmentalists propose a contextual reason. They maintain that complex networks of ecological relationships may be disrupted by the extinction of component species and that such disruptions may have widespread and unpredictable repercussions. Those repercussions may be economic or aesthetic, but they may also be biological, possibly to the extent of reducing the capacity of the global environment to sustain humans. Is this feasible? No one can say.

Whatever the reason, most people accept that the conservation of wildlife is desirable. Achieving this objective is difficult, requiring a much deeper understanding of the natural world than we possess at present. Nevertheless, we must do what we can with such knowledge as we have, and there have been successes to encourage us.

58 Zoos, nature reserves, wilderness

Zoos have had a curious history. They began as menageries, collections of living wild animals made for various reasons. In the twelth century BC, the Chou dynasty emperor Wen maintained a collection of animals from all parts of the Chinese Empire, presumably to reflect his authority over far-flung regions with exotic fauna. Ancient Mesopotamian (FOSTER, 1999) and Egyptian rulers were especially keen on menageries and the Romans maintained huge collections, many for use in gladiatorial combat. A few ancient menageries were used to study animals, but the great majority served only as entertainment or as a source of impressive animals, often large cats, to emphasize the political power of their owner. The menagerie established by the English king Henry I (1100–35) at Woodstock, in Oxfordshire, was later moved to the Tower of London and taken from there, in 1829, to form the nucleus of the collection at Regent's Park Zoo.

Wherever zoos were opened to the public they became highly popular but, despite assertions of their educational value, they remained entertainments. The zoo was a place where parents could spend a fine afternoon with their children. To make them clearly visible at close quarters, the animals were often housed in cramped and quite unsuitable accommodation. In modern times this has led many people to denounce zoos as 'prisons' in which wild animals are cruelly confined for no valid reason.

Unfortunately there remain some disreputable zoos that justify such criticism, but the reputable zoos exist today primarily for conservation purposes. Zoos remain open to the public, partly because nowadays they really do offer educational facilities but more importantly because they depend on entrance charges to help with their operational costs. Keeping wild animals, adapted to markedly different climates and diets, is an extremely expensive business.

Botanic gardens have a parallel history. They too have developed from collections of exotica gathered by plant collectors. After appropriate acclimatization and development, many became popular garden cultivars. Nowadays, botanic gardens are also concerned primarily with conservation.

Plants and animals are protected while they remain within botanic gardens, zoos, and aquaria. If they can be bred in captivity, then it may be possible to reintroduce species to places where they have become extinct or where surviving populations are declining. There have been successful reintroductions, but there have also been failures. In the 1970s, for example, the Hawaiian goose, or ne-ne (*Branta sandvicensis*), was apparently rescued from extinction by a captive breeding programme from a small stock held by the Wildfowl Trust at Slimbridge, England, and funded by the Worldwide

Fund for Nature (WWF). More than 1600 birds were released on the islands of Hawaii and Maui and the WWF claimed the release as a success (STONEHOUSE, 1981, p. 96). By the early 1990s, however, only four birds survived from the 1600 released (RAVEN *ET AL.*, 1993, p. 360). The failure was probably due to the restricted gene pool represented by the small breeding stock. The geese succumbed to inbreeding depression. Reintroductions are also likely to fail if the pressures leading to the decline of the wild population continue to operate or if, in the absence of the wild population, the habitat has been altered in ways that render it no longer hospitable. Even where these criteria are satisfied, there is a danger that in the course of its captive breeding a species will have been modified in ways that reduce its ability to survive in the wild. Animals are usually prepared for release, essentially by teaching them how to find food, shelter, and mates. Care must also be taken to ensure that captive-bred individuals do not carry diseases, acquired in captivity, to which they but not the wild populations are immune.

Questions also arise over precisely what is being captively bred for reintroduction. In the light of modern genetic understanding, the species concept is inadequate if the aim is to maintain as high a level of genetic diversity as possible. Breeding programmes for both plants and animals now involve karyotyping, the comparison of chromosomes. This can reveal differences between populations of the same species. It has led to the recognition, for example, of two genetically distinct populations of orang-utan separated by a geographical barrier, although both belong to the same species, *Pongo pygmaeus*. The distinction will be lost if the two interbreed, so it is important to reintroduce purebred individuals to their native populations. It has been discovered that more than 20 per cent of orang-utans in zoos are hybrids of the two populations and so, despite the rarity of this species, they are not permitted to breed (TUDGE, 1993, pp. 267–268). 'Genetic finger-printing' is also used to categorize organisms in fine detail.

Zoos and botanic gardens do not have unlimited space to keep whole plants and animals, but there are other ways in which species can be conserved. Suitable restriction enzymes make it possible to cut DNA into small fragments which can be recombined with plasmids and inserted into bacteria that are then cultured. This technique can be used to store, as fragments, the entire genome of selected individuals as a genomic library (TUDGE, 1993, p. 212). At present it is not possible to reconstruct individuals from such a store, but one day it may become so and meanwhile their genetic material is secure.

Many rare or endangered plants are preserved in seed banks, where seeds are desiccated to a water content of about 4 per cent and stored at 0°C, the quality of the seeds being checked from time to time by germinating them. Stored seeds usually remain viable for 10–20 years. Of course, the security of the plants depends on that of the store and there are fears that lack of funds threatens to make some seed banks into 'seed morgues' because of staff shortages and, in some cases, too small a quantity of seeds to warrant the risk of thawing and attempting to germinate them (FINCHAM, 1995). 'Recalcitrant' seeds cannot be treated in this way, because desiccation destroys them and they can be stored for only a few days. Where possible they are preserved as growing plants, but in some cases they can be held more economically as tissue cultures.

Nature reserves offer a different approach to conservation, protecting habitats directly and the species occupying them by implication. There has been much debate among ecologists over the relative merits of the wide variety of features that may qualify an area for protection as a reserve. One widely accepted aim is to establish a set of reserves representative of every type of habitat within a country or region, sites being selected on the basis of their flora, fauna, or geological features. Reserves may be publicly or privately owned and managed by agencies of national or local government or by voluntary bodies. In Britain, the Royal Society for the Protection of Birds, the Royal Society for Nature Conservation and its affiliated county naturalists' trust in England and Wales, and the Scottish

Wildlife Trust manage many hundreds of nature reserves. Because they exist solely to conserve valued areas, public access to reserves may be controlled or denied, although open public access is allowed wherever possible.

Reserves vary greatly in size, mainly because sites are acquired as opportunity arises in the form of patches of land for which landowners have no commercial use or which they are prepared to relinquish out of sympathy for the aims of conservationists. Although this is clearly the best that can be achieved, and implies no criticism of them, the somewhat haphazard patchwork of small, isolated reserves that results might be thought unsatisfactory. The link between habitat fragmentation and species extinction is well established and suggests that in the case of nature reserves, the bigger the better.

It is not necessarily so, and ecologists have not yet resolved what has been nicknamed the 'SLOSS' debate, 'SLOSS' being an acronym for 'single large or several small'. There is no general answer. Some species, such as grizzly bears and tigers, require large areas, and a large reserve is likely to support a greater number of species than a small one.

The choice, though, is not between large or small areas, but between one large reserve or several small ones with the same combined area. If small reserves are preferred, a further choice must be made, illustrated in Figure 6.3. Should the reserves remain isolated, like islands, or should they be linked by corridors? Ecological studies of actual islands and of 'islands' produced when habitats are fragmented have provided information that will provide guidance in particular situations. In the Brazilian Amazon, the fragmentation of forest into isolated patches was followed by a doubling in the number of frog species, and after seven years in their patches they seemed to be thriving. Bird and insect numbers declined, however (CULOTTA, 1995a). It has also been found that compared with a single large reserve of the same area, several small reserves between them support more species of mammals and birds in East Africa, mammals and lizards in Australia, and large mammals in the United States (BEGON *ET AL.*, 1990, pp. 790–791).

Should 'island' reserves be isolated or linked by corridors? Since small, isolated populations may be prone to inbreeding, corridors that are ecologically similar to the islands may provide opportunities for migration, thus increasing outbreeding. In Britain, hedgerows have often been described as corridors, ecologically resembling woodland edge, linking isolated patches of woodland, and have been valued for that reason, but there is little reason to suppose they are used for migration. Corridors are narrow and an animal might be wary of moving along one for fear of predators in the hostile environment to either side. The exception to this might be large



Figure 6.3 Island wildlife refuges

predators themselves. They routinely travel considerable distances and corridors would conveniently guide them to prey more or less trapped in the islands. Diseases and parasites might also move along corridors (BREWER, 1988, p. 636). These considerations do not detract from the value of corridors used to link otherwise separated parts of the same range. Conduits built beneath roads for the use of migrating toads and of mammals patrolling their ranges have proved very effective at reducing road fatalities.

Nature reserves protect relatively small areas of habitat. National parks protect very large areas. National parks were defined by the IUCN (International Union for Conservation, Nature and Natural Resources) in 1975 as large areas of land that have not been altered materially by human activities and are of scientific, aesthetic, educational, or recreational importance. They are managed by the state, and the public are welcome to visit them provided their activities do not conflict with conservation policies. British national parks, which were designated before the IUCN definition was written, are rather different in that most of their area is privately owned and farmed. National parks are large enough to meet the needs of many species, but even they are not big enough for some. The Yellowstone National Park, occupying almost 9000 km², may not provide sufficient space for its grizzly bear population and for this reason it has been proposed to link the park to several national forests and the Red Rock Lakes National Wildlife Refuge to produce a 'greater ecosystem' (BREWER, 1988, p. 637).

Finally, entire areas of wilderness may be afforded protection. A wilderness is an extensive tract that has never been occupied permanently by humans or used by them intensively and so exists in something close to a natural state. Such areas are rare in Europe, but less so in North America and other continents. Their protection includes a prohibition on the construction of roads into or through them and controls on the number of people visiting them at any one time.

Natural communities or living organisms are not static. Left to itself, a nature reserve, national park, or in some cases even a wilderness area will gradually change. Species will disappear and others replace them, possibly altering radically the character of the entire system. When grassland, including prairie, is protected from grazing and fire, for example, it tends to develop into scrub and eventually forest. This raises yet another controversy among conservationists, some holding that protected areas should be allowed to develop naturally, others that they should be managed so that they continue to support the species by which their value was defined in the first place. People who believe areas should remain unchanged from the condition they were in when their importance was first recognized are sometimes described as 'preservationists' and contrasted with 'conservationists', who seek to prevent industrial and urban development that would destroy or degrade habitat, but not to interfere unduly with other ecological changes which occur naturally.

In practice, most reserves and parks are managed. Management may involve such tasks as culling species that become too numerous, clearing waterways of plants that might choke them and deplete the amount of oxygen dissolved in their water, and allowing natural fires to take their course or even firing areas deliberately.

Different as they are, all these approaches to species conservation share the same objective and complement one another. Seed banks, gene banks, and genomic libraries store the genetic diversity of living organisms under strict control and without occupying land that might be converted to other uses regardless of the protests of conservationists. Zoos, aquaria, and botanic gardens store living plants and animals for purposes of study and, albeit controversially, as a source of individuals for reintroduction. Operating at different scales, nature reserves, national parks, and wilderness areas conserve entire biological communities.

On 1 March 1872, Yellowstone became the first national park in the world. Since then much has been learned about the need for conservation and the most appropriate means for achieving it. Scientists and managers are still learning, now more rapidly than ever before, and we may anticipate that in years to come conservation methods will continue to advance.

59 Pest control

Farmers have always had to contend with pests which feed on their crops in the field or after harvest, and for many years they have relied mainly on toxic chemicals to achieve a satisfactory level of control. In the 1930s the principal substances used were based on nicotine, arsenic, and cyanide. They were highly dangerous to humans and to wildlife, but evoked no public alarm, although crime writers were fond of using 'weedkiller' as a fictional murder weapon. A new generation of organic compounds began to replace them in the 1940s. These were much less toxic to mammals. DDT is about as poisonous to humans as aspirin, but it is a great deal more difficult to ingest a lethal dose of it.

Problems with the new insecticides soon started to emerge. As early as 1945, scientists suspected that DDT might have an adverse effect on wildlife and in 1947 seven British workers died of poisoning after working with DNOC (dinitro-*ortho*-cresol). This led to legislation controlling pesticide use, in the Agriculture (Poisonous Substances) Act 1952. During the 1950s the effects on wildlife increased and in 1961 certain substances used as seed dressings, to prevent fungal infestation of seeds prior to germination, were withdrawn (CONWAY *ET AL.*, 1988). The publication of Rachel Carson's *Silent Spring* (CARSON, 1963), in 1962 in the United States and 1963 in Britain, aroused public awareness of the hazards associated with insecticide use, but it told scientists nothing of which they were not already aware and irritated many of them by exaggerating the seriousness of the problem.

That problem arose primarily from the biomagnification, or bioaccumulation, of chemically stable compounds as they passed along food chains, but also from their lack of specificity. Organochlorines, the first generation of organic insecticides, of which DDT is the best-known member, succeeded partly because of their persistence. Once applied, the insecticide remained on and around crop plants, to poison any insects that came into contact with it. Predators eating prey exposed to a sublethal dose accumulated the insecticide until it reached harmful concentrations. At the same time, organochlorine compounds were toxic to a wide variety of arthropods. As well as killing members of pest species they also killed arthropod predators of those species.

As Figure 6.4 shows, however, the agricultural effect of the new pesticides was dramatic. Yields rose sharply and post-harvest losses fell. In the tropics, where the climate makes food storage much more difficult than in temperate climates, rodents, insects, and fungi can destroy 8 per cent of stored potatoes, 25 per cent of cereal grains, 44 per cent of carrots, and 95 per cent of sweet potatoes before they reach the market (GREEN, 1976, p. 98).

DDT was first used not in food production, however, but to control such insect vectors of disease as the human body louse (*Pediculus humanus corporis*), which transmits typhus, and the *Anopheles* mosquitoes that transmit malaria. In 1946 there were 144000 cases of malaria in Bulgaria and in 1969 there were 10, in Romania the number of cases fell from 338000 in 1948 to 4 in 1969, and in Taiwan from 1 million in 1945 to 9 in 1969 (GREEN, 1976, p. 100). DDT is still used in some countries against malaria mosquitoes, but its effectiveness is restricted by the number of species that have become resistant to it. As early as 1946, houseflies in northern Sweden were immune to DDT and by the 1950s mosquitoes and lice were becoming immune in southern Europe and



Figure 6.4 **Pesticide use and crop yield** Source: Green, M.B. 1976. Pesticides: Boon or bane? Elek Books, London

Korea (MELLANBY, 1992, pp. 53–60). It was estimated that in 1980 the world was spending almost US\$640 million a year to control insect disease vectors, yet 100 million new cases of malaria occur every year and almost 1 million people die (ABRAMOV, 1990).

Taken together, the adverse effects on wildlife and rapid acquisition of resistance by pest species have led many people to speculate about the possibility of abandoning entirely the use of chemical pesticides. This has not happened, of course. In 1986–87 British cereal farmers spent £110 million on herbicides, £85 million on fungicides, £4 million on insecticides, and £15 million on the treatment of seeds (TYSON, 1988). There are now literally hundreds of pesticide compounds on the market.

Alternatives to the chemical control of pests have been developed, but in parallel with developments in the formulation and application of pesticides themselves. Predictably, the highest environmental impact resulted when broad-spectrum poisons were pumped from sprayers not very different from lawn sprinklers. Crops were drenched with huge quantities of pesticide. The upper surfaces of leaves were thoroughly coated, but the undersides were largely missed and most of the pesticide fell to the ground where it poisoned harmless or beneficial organisms and could drain into waterways—and in mosquito control programmes insecticide is sprayed directly on to the surface of stagnant water to kill larvae. Pesticides also travel by air, forming microscopic aerosols that can be carried long distances.

Over the past twenty years all the industrialized countries have banned or severely restricted the agricultural and horticultural uses of organochlorine compounds. Traces of them still remain in the

environment, because of their great stability, but concentrations are very low. They have been detected in ground water at more than 0.1 parts per billion in some parts of Britain (TYSON, 1988) and minute traces, at the very limit of measurement, have been found in rivers in Northern Ireland, but there they are believed to have come from the domestic use of wood preservatives, not from farms or factories (MASON, 1991, p. 179). They have been replaced by progressively more specific compounds, designed to poison only target species. At the same time, new pesticides are required to undergo very rigorous environmental testing before they are licensed for use. Testing can take five to ten years from the time a potentially useful compound is identified, during which time its fate must be traced in the soil, air, and water of every environment in the world in which it is likely to be used. Once it is marketed, its environmental effects continue to be monitored (ALLABY, 1990, pp. 36–37).

More efficient application methods were also sought. The most promising of these were based on ultra-low-volume (ULV) sprayers. Some worked electrostatically, but in the simplest the pesticide is pumped from a reservoir on to the centre of a toothed disc, resembling a cog-wheel. The disc spins, spreading the pesticide to the edge where it flows along the teeth, leaving the disc as a fine stream that quickly breaks into minute droplets all of much the same size (see Figure 6.5).



Figure 6.5 Even-sized droplets from the teeth of an ultra-low-volume pesticide sprayer
The droplets form a mist that drifts into the crop, coating all surfaces of the plants but without contaminating the ground. The sprayers themselves are made from plastic, the pump driven by a torch battery, and the discs can be changed to alter the size of the teeth and thus the size of the droplets, as appropriate to the pesticide and crop (see Figure 6.6). ULV sprayers achieve better pest control than conventional sprayers and use 1–10 per cent of the amount of pesticide. They must be used with care, because they require a more highly concentrated pesticide solution and so expose the operator to greater risk, but compared with other sprayers their environmental impact is greatly reduced.

Biological control offers an entirely different way of dealing with pests. It has been applied most widely to glasshouse crops, because it is in glasshouses that pests cause the most serious damage and where they most rapidly acquire resistance to insecticides. In the best-known method, the pest is attacked by its own natural parasites and predators, bred for the purpose and introduced. First, the pest is introduced to the crop and allowed to become established. This provides a food supply for the predator or parasite, which is introduced next. The pest is not eliminated, but once its population is reduced to an economically tolerable level the pest's own enemies prevent it from increasing. A range of agents for biological control are now produced on an industrial scale in many countries to deal with a number of species of mites, aphids, thrips, caterpillars, mealybugs, and others. Other pests are controlled by bacteria, fungi, nematodes, protozoa, and viruses. By 1986, 63 per cent of British glasshouse-grown cucumbers were being protected biologically from two-spotted mites and 55 per cent from whitefly, and 14 per cent and 43 per cent of tomatoes from those two pests respectively. Biological control is also used, but to a smaller extent, in fruit orchards (PAYNE, 1988).

The sterile male technique has been used against the screw worm, a fly that attacks cattle, various fruit flies, tsetse fly, cockchafer, codling moth, onion maggot, and others (LACHANCE, 1974). It involves breeding the pest species, separating the males, and sterilizing them, usually by irra-diation. Then they are released to mate unproductively with females, which lay unfertilized eggs.

Pheromones are used to trap certain pests. These are chemical attractants by which males and females locate one another for mating. Synthetic pheromones released in the right place at precisely the right time draw large numbers of insects into traps, where they can be killed.



Figure 6.6 A hand-held ultra-low-volume sprayer

Integrated pest management

Modern pest control uses all appropriate methods, including pesticides, but is based primarily on detailed knowledge of the life cycle and behaviour of the pest. Its aim is not to eradicate the pest, but to control its population at a level below that at which economic damage becomes intolerable. It is often called integrated pest management.

The pea moth (*Cydia nigricana*) mates in summer. Its eggs hatch after 9–16 days and the larvae quickly bore into pea pods. They spend three weeks there, feeding, then fall to the ground, make cocoons, and remain in the soil until they emerge as adults the following year. They are especially vulnerable to insecticide during the 24 hours between hatching and entering pods.

Prior to mating, females attract males by releasing a scent (a pheromone). This substance has been analysed and synthesized. The synthetic pheromone is placed in traps with sticky floors, located among the rows of peas, and the grower checks the traps every day while the pea plants are in flower. On the day the traps are full of male moths, the grower knows eggs are about to be laid and, therefore, larvae will start emerging 9–16 days later. The crop is sprayed twice, one week after the males are found in the traps and again three weeks after that.

The lygus bug (*Lygus hesperus*), a serious pest of cotton, is dealt with in a similar way, by using nets to sweep the crop in search of the insects. When the ratio of bugs to cotton buds exceeds a certain threshold, the crop is sprayed.

These are examples of integrated pest management (IPM). Its success requires detailed knowledge of the pest and its ecology, and workers trained to monitor populations reliably. These difficulties are not insuperable, but they have delayed the widespread adoption of IPM.

Synthesized compounds that mimic juvenile hormones have also been tried. Juvenile hormones are produced by insects while they are immature. When they cease to produce them they mature. If they are exposed to compounds with a similar effect, they fail to mature and so do not mate.

Pests, weeds, and plant and livestock parasites must be controlled. In the world as a whole, the need to increase the amount of food available means that losses from all causes must be minimized. Even in the industrialized countries, where farmers are capable of producing more food than their own markets demand, a relaxation of control would not be acceptable. As yields fell, more land would be needed for cultivation, and it is the practice of agriculture itself that has the most serious effect on wildlife habitats and the environment generally. Reduced yields would also mean that food prices would rise. Abandoning control is not an option and would not necessarily bring any environmental improvement.

This means that pesticides will remain in use for many years to come, but in reducing amounts of less environmentally hazardous compounds. Better application methods will allow adequate control to be achieved with less pesticide, and alternatives to chemical control, including those made possible by genetic manipulation, will become available for an increasing range of targets. Meanwhile, pesticides themselves are far more specific than they were and great care is taken to ensure they cause no harm to non-target species.

In the past, pesticides have caused environmental damage. This is already much reduced and in the future we may expect it to fall still further. These necessary improvements have resulted from detailed studies of the biology and ecology of pest species that allow infestations to be identified early and the pests to be attacked with considerable precision. Increasingly, the development of crop varieties that are genetically modified to render them tolerant of herbicides and resistant to insect pests and to viral and fungal diseases will allow the use of pesticides to decline in years to come.

60 Restoration ecology

Environmentalists sometimes complain that once an area becomes degraded and its environmental quality reduced, it is lost for ever. This makes a good campaigning argument, but it is untrue. Many environments will recover naturally in time and others will develop into new environments no less interesting and valuable than those they have replaced. Long-abandoned quarries are often of considerable ecological and geological interest. Even land poisoned by industry may eventually acquire new ecological value. Until 1919, for example, household washing soda was manufactured by the Leblanc process. The British soda industry was concentrated in Lancashire, where it caused appalling air pollution and generated large amounts of toxic and very alkaline wastes, with a pH of nearly 14. These were dumped, in some places forming a layer several metres deep. Then the Leblanc process was replaced by the Solvay process. This also produces alkaline wastes, but they have been disposed of more carefully. After seventy years, the old Leblanc waste sites have weathered until now they support a wide variety of lime-loving plants, including many orchids, and are of considerable botanical importance (MELLANBY, 1992a, pp. 64–66).

Human intervention can restore other sites to their original state, or to something closely approaching it, or rehabilitate them to a state different from the original, but much better than their degraded state. Spoil heaps from mining can be transformed into areas supporting a rich flora appropriate to the surrounding environment, but not necessarily identical to the communities the land supported originally.

Restoration and rehabilitation call for a detailed understanding of community ecology. In most cases, ecologists concentrate on plant ecology, because if viable plant communities can be established animals typical of such communities will enter them of their own accord. The branch of ecology specializing in this work is called restoration ecology (*darwin.bio.uci.edu/~sustain/EcologicalRestoration/index.html*) and it has been described as the 'acid test' for ecology, because it calls on ecologists not simply to take ecosystems to pieces to see how they work, but to assemble them and make them work (BEGON *ET AL.*, 1990, p. 607).

Restoration ecologists all over the world are watching the progress of the largest restoration project ever attempted. If it succeeds there are many places where it may be repeated. It began in the mid-1990s in the Everglades.

At one time, most of this large area in southern Florida (see Figure 6.7) was flooded for at least eight months of the year and much of it for more than that. Every year, during the wet season Lake Okeechobee overflowed and water flowed slowly south in what was effectively a river 80 km wide and less than 1 m deep, covered in algae and passing through swathes of saw grass. It was called a 'river of grass'. The swamp environment was rich in wildlife but inhospitable to humans, and about half the area was drained early in this century. Then, in the 1960s, the US Corps of Engineers began building 1600 km of channels with levees to carry the water away more quickly, some of it to be stored in 'water conservation areas'.

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Figure 6.7 Florida, showing the location of the Everglades

No one predicted the extent of the consequences. The marshes dried, and became more saline, and populations of wading birds and other vertebrates fell by up to 90 per cent. Water in Florida Bay became anoxic, threatening fish stocks, and it was feared that if the depletion of aquifers continued it might lead to water shortages in the cities they supply.

Restoration involves lowering the levees, changing the straight channels back into river meanders, and eventually, over the next 15–20 years at a cost of about \$2 billion, returning the area to natural wetland that floods and drains according to the rainfall. The work is being carried out by the Corps of Engineers in collaboration with a number of federal and state agencies and the Everglades National Park, and it proceeds slowly and cautiously. It is especially important to monitor closely the quality of the water that is released to flow into the area. If the water is polluted, the contamination could affect a wide area and wildlife would not return. Basing the operation on 'adaptive management', the planners deal with one small area at a time and make a minor change then wait to see what happens before proceeding further (CULOTTA, 1995).

Not all restoration involves major environmental engineering. It can be subtle and invisible to the naked eye, especially where the purpose is to remove pollutants by 'bioremediation'. The industrial detergents used to emulsify the crude oil after the first major oil-spill incident, when the *Torrey Canyon* went aground off the Isles of Scilly in 1967, may have done more harm to marine organisms than the oil itself. Since then much has been learned about the fate of oil in the sea. In particular, it has been found that over 30 genera of bacteria and fungi feed on hydrocarbons, converting them to

carbon dioxide, water, and their own cell matter. These microorganisms are common in most environments and as long ago as 1973 some biologists were suggesting their help might be enlisted in dealing with oil spills. There were several successful trials, but it was not until March 1989 that this idea could be really tested. That was when the *Exxon Valdez* spilled 41 million litres of crude oil into Prince William Sound, Alaska, contaminating approximately 2000 km of the intertidal zone along the rocky coast.

No microorganisms were introduced, but the growth of those already present was stimulated by adding fertilizer to provide the nutrients the oil could not supply. The fertilizer, amounting to about 50 tonnes of nitrogen and 5 tonnes of phosphorus, was applied in the summers between 1989 and 1992. Careful monitoring and comparisons between treated and untreated sites indicated that the treatment was effective, produced no adverse side-effects, and that it might have been even more successful with higher fertilizer applications (BRAGG *ET AL*., 1994).

Plants can also be used to remove pollutants. Reed beds are being established in some places to purify water before its discharge into rivers or lakes. The reeds (*Phragmites communis*) are planted into gravel or soil in a pit sealed with an impervious liner. The plants transport oxygen to the root area, where water flowing through the pit is purified by aerobic bacteria, solid wastes are composted in the layer of dead leaves and stems from the reeds, and water is treated by anaerobic bacteria in the surrounding soil (MASON, 1991, p. 69). Reeds are used in this way to treat sewage, nutrient-enriched water leaching from farmland, and water contaminated with metals that drains from abandoned mine workings.

This use of plants is called 'phytoremediation' and it can also be applied in terrestrial habitats. *Brassica juncea*, a variety of mustard, accumulates such metals as selenium, cadmium, nickel, zinc, chromium, and lead. Under field conditions, after several years it had reduced selenium levels by up to 50 per cent in the uppermost metre of soil.

In trials at Rothamsted Experimental Station, England, alpine pennycress (*Thlaspi* caerulescens) was found to accumulate zinc and cadmium until these metals accounted for several percent of the weight of the plants. *Thlaspi caerulescens* can tolerate the poisons because it and other plants produce phytochelatins, small peptide molecules that bind metals in less toxic forms and, in some plants, transport them into cell vacuoles where they are stored safely. Mercuric reductase, an enzyme that detoxifies mercury, is produced by certain bacteria, and the gene encoding it has been transferred to *Arabidopsis thaliana* (thale cress) plants. Thus transformed, the plants grew in a solution of mercuric chloride that killed other plants. They convert the mercuric chloride into elemental mercury, which they release slowly into the air as mercury vapour, at what biologists hope are harmless concentrations. Selenium is also released into the air by cabbage, broccoli, and some other plants, as dimethyl selenide, which is harmless (MOFFAT, 1995).

Plants with phytoremediation potential are especially common in the tropics and subtropics, possibly because the toxic metals protect them against herbivorous insects and microbial parasites. There is a risk that the plants might also poison small mammals, but on contaminated land, where they would be grown, those mammals are already in danger. The plants are harvested and are then either dried and buried, or burned. Energy from the burning of the biomass fuel can be sold and the ash from them contains the metals they accumulated. Some of these are of commercial value and can be sold. Sales of energy and metals offset much of the cost of this treatment and may even make it profitable. This is the technique currently used to treat contaminated soil. Dried plants and ash have much less mass than the soil from which the metals were removed, so if they cannot be sold burying them costs much less than excavating the soil and disposing of it.

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Plants can be used to obtain metals, including thallium and gold, from low-grade deposits. This is called 'phytomining' and it causes far less environmental disturbance than conventional mining (BROOKS *ET AL*., 1999).

Excavation and burial is the alternative to phytoremediation for restoring mine spoil and tailings heaps and many abandoned industrial sites. Antinuclear campaigners often criticize the cost and technical difficulties inherent in the decommissioning of nuclear plants that have reached the end of their useful lives, but these are well known and modest compared with the those of decommissioning other industrial installations.

At Oakville, Ontario, in 1983, falling demand for petroleum led to the closure of a Shell refinery that had been processing 44000 barrels (about 8 million litres) of oil a day. It took Shell six years and cost an estimated Can\$4 million to restore the 222-ha site to residential and commercial use. All the remaining oil was removed and the plant and buildings dismantled. Wells were dug to monitor ground water, the soil was analysed and either treated to clean it or excavated and removed, and the soil population studied to determine whether the soil could support plants. This was the first refinery site to be restored, but it will not be the last (ALLABY, 1990, p. 102).

At one time, factories were not decommissioned when they were no longer needed; they simply closed, often because they had failed and their owners were bankrupt. Anything that could be sold was removed, but the rest was left to decay. Even if the buildings found new uses, no thought was given to the ground around them, where for many years metals may have been stored and chemicals spilled. In the early 1990s, the British government proposed the compilation of a register of such industrially contaminated land at 100000 sites. When it was realized that this would seriously inhibit attempts to regenerate inner cities by developing those sites, the scope of the proposed register was first reduced and finally, on 17 February 1993, the plan was abandoned altogether. Much of the environmental degradation we are now trying to remedy has been inherited for this reason. The problem will diminish over the years, as old sites are restored, and under present planning laws permission for the industrial use of land is not granted unless a detailed, funded scheme for site restoration is included in the application, with firm assurances that it will be implemented.

Restoration ecology, and the bioremediation and phytoremediation techniques it employs, make this a practicable requirement. As restoration ecologists learn more about the way viable biological communities can be established on previously degraded land, even the most recalcitrant sites may recover. At the same time, restoration ecology provides the understanding that allows restoration plans to be structured into the life history of present and future industrial operations.

61 World conservation strategies

By the late 1960s it was clear to those engaged in the emerging environmental movement that the world faced problems which could be resolved only at a global level, an idea that quickly resonated with public opinion. The issues arising from the combined effects of population growth, resource depletion, and environmental degradation, were explored in countless books and articles and summarized, perhaps most lucidly, by Paul and Anne Ehrlich in *Population, Resources, Environment,* a book they published in 1970 with a revised edition in 1972 (EHRLICH AND EHRLICH, 1972). 'A Blueprint for Survival', published as the entire January 1972 issue of *The Ecologist* magazine (GOLDSMITH *ET AL.*, 1972), attracted much attention, as did *The Limits to Growth*, the popular report of a computer model of the world, sponsored by the Club of Rome and also published in 1972 (MEADOWS *ET AL.*, 1972).

Such publications reflected the intense intellectual fervour that formed the background to the first major conference on a single topic to be held by the United Nations, in Stockholm in June 1972. The UN Conference on the Human Environment was attended by delegations from almost all member states, with the exception of the USSR and its East European allies, as well as non-governmental groups, who held meetings and events of their own. A team from *The Ecologist* and Friends of the Earth published a daily newspaper, *The Stockholm Conference Eco*, which was distributed by bicycle to the hotels where delegates were staying; after its first few days permission was granted for it to be handed out in the conference centres.

A book setting out the issues to be debated was commissioned by the Secretary-General of the conference, Maurice Strong (WARD AND DUBOS, 1972). Somewhat less apocalyptic in tone than other environmentalist literature, it ended with a chapter on 'strategies for survival'. This emphasized the need for sovereign nations to collaborate in research and programmes of action. 'If this vision of unity—which is not a vision only but a hard and inescapable scientific fact—can become part of the common insight of all the inhabitants of Planet Earth, then we may find that, beyond all our inevitable pluralisms, we can achieve just enough unity of purpose to build a human world' (WARD AND DUBOS, 1972, p. 297).

The Stockholm Conference produced a Declaration on the Human Environment, adopted by the General Assembly in 1973, and led to the establishment, also in 1973, of the UN Environment Programme (UNEP), based in Nairobi. This was an entirely new UN agency, charged with coordinating global monitoring of the environment and international programmes for environmental improvement. Over the more than twenty years of its existence, UNEP has brokered treaties and conventions on a wide range of topics, from pollution reduction in partially landlocked seas (the Regional Seas Programme) to the 1987 Montreal Protocol on Substances that Deplete the Ozone Layer, and the 1992 United Nations Framework Convention on Climate Change (*www.unfcc.de/*) with the Kyoto Protocol that was added to it in 1997.

Progress was clearly being made, but there was still no broad framework of defined objectives against which individual schemes could be evaluated. The task of developing one was assumed by the International Union for Conservation of Nature and Natural Resources (IUCN), based in Switzerland, with Robert Allen, a former editor of *The Ecologist*, as its compiler and editor. A large team of ecologists, conservationists, and writers contributed ideas and outlines. UNEP and the World Wildlife Fund (WWF, now the Worldwide Fund for Nature) cooperated and gave financial assistance, and the document was prepared in collaboration with the Food and Agriculture



Figure 6.8 Living resources and population Source: World Conservation Strategy, Introduction: Living resource conservation for sustainable development. IUCN, UNEP, and WWF, 1980

Organization of the UN (FAO) and the UN Educational, Scientific and Cultural Organization (UNESCO). The result was the World Conservation Strategy: Living Resource **Conservation** for Sustainable Development (IUCN, 1980), published in March 1980 as an Executive Summary, Preamble and Guide, and Map Section, as separate booklets accompanying the World Conservation Strategy itself, all contained in a folder. It was directed to government policy-makers and their advisers, conservationists, and all those involved professionally in economic development.

The *World Conservation Strategy* took as axiomatic what by then had become the orthodox environmentalist diagnosis, that as human numbers continue to in-crease, each person will



Figure 6.9 Resource consumption by rich and poor Source: World Conservation Strategy, Introduction: Living resource conservation for sustainable development. IUCN, UNEP, and WWF, 1980

be entitled to a dwindling share of the resources upon which human life depends. This prognosis was presented graphically as a man growing bigger between 1980 and 2020, while a tree and wheat plant beside him grew smaller (see Figure 6.8). It also pointed out that access to resources is not shared equally, again illustrated graphically as 1 Swiss person being equivalent to 40 Somalis in terms of resource consumption (see Figure 6.9).

Having outlined problems arising from the loss or degradation of agricultural soils, forests, coastal wetlands and freshwater systems, and genetic diversity, the *Strategy* set out a list of objectives and action that might be taken at the national and international level. This included a recom-mendation that each country produce a national or several subnational strategies of its own, modelled on the *World Strategy*.

Britain was one country which did. Following the pattern of the *World Conservation Strategy*, it was published in 1983 as three documents: a brief summary, an overview, and the the full report of nearly 500 A4 pages (WWF *ET AL*., 1983). The British response dwelt on the 'post-industrial society' that appeared to be emerging and urged the rebuilding of those industries which meet 'real' domestic and export needs (WWF *ET AL*., 1983, para. 7). It based this call on its judgement of the position of the economy in the fourth Kondratieff cycle. This was the approximately 50-year alternation of periods of prosperity and decline identified by the Russian economist Nikolai Kondratieff (1892–*c*. 1931), illustrated in Figure 6.10. At the time the report was prepared, the British economy was clearly in decline and it was only by assuming the validity of the Kondratieff model that the point could be estimated at which full-scale depression would be reached and followed by recovery. What the model did show, however, was a slow but steady economic advance which meant people were a little more prosperous at each peak and a little less poor at each trough than they had been at the peak and trough of the preceding cycle.

Both reports sought ways to achieve steady economic growth without causing injury to the natural environment, especially the countryside and wildlife, and without so depleting the resources on which industry and human welfare depend as to block growth at some time in the future. They



Figure 6.10 Kondratieff cycles After Introduction to The Conservation and Development Programme for the UK. 1983. Kogan Page, London

also recognized that the gap between rich and poor countries, and groups within countries, must be reduced if the global environment is to be protected adequately. The most acute problems were seen to reside in the less developed regions of the world. Without development poverty would continue to exacerbate them.

This view provided the starting point for another influential report that approached the world situation from a different point of view. The Brandt report (INDEPENDENT COMMISSION ON INTERNATIONAL DEVELOPMENT ISSUES, 1980), produced by a commission of senior politicians and economists led by Willy Brandt, a former chancellor of West Germany, drew attention to the pressure on resources that could result from population increase (INDEPENDENT COMMISSION ON INTERNATIONAL DEVELOPMENT ISSUES, 1980, pp. 105–116), although it did not predict a depletion of mineral resources generally, only of oil supplies. It argued that economic development could trigger a demographic transition, and was concerned about the large-scale migrations it believed population growth would cause and the fate of migrants. It diagnosed the economic disparity between rich and poor as the gravest problem facing the world and its elimination through development as the solution. Its recommendations were directed to this end.

The *World Conservation Strategy* and its British sequel placed great emphasis on 'sustainability'. This was not a novel concept, but they drew it to the attention of the politicians to whom their reports were addressed, and it was the report of yet another international commission (WORLD COMMISSION ON ENVIRONMENT AND DEVELOPMENT, 1987) that finally brought the word into common use. The World Commission on Environment and Development, or Brundtland Commission after Gro Harlem Brundtland, its leader, drew together and aimed to reconcile the two strands of environmental conservation and economic development, and supplied what came to be the generally accepted definition of 'sustainability': 'Sustainable development is development that meets the needs of the present without compromising the ability of future generations to meet their own needs' (WORLD COMMISSION ON ENVIRONMENT AND DEVELOPMENT, 1987, p. 43). 'Sustainable development', the Report said a few pages later, 'requires the conservation of plant and animal species.... [and] requires that the adverse impacts on the quality of air, water, and other natural elements are minimized so as to sustain the ecosystem's overall integrity.' This led to an expansion of the definition:

In essence, Sustainable development is a process of change in which the exploitation of resources, the direction of investments, the orientation of technological development, and institutional change are all in harmony and enhance both current and future potential to meet human needs and aspirations (WORLD COMMISSION ON ENVIRONMENT AND DEVELOPMENT, 1987, p. 46).

Although difficult to define in more precise economic terms, the concept of sustainable development quickly became a necessary ingredient of all papers and reports dealing with the environmental implications of economic development and industrialization. It was central to the preparations made for the sequel to the Stockholm Conference, held in 1992. In the twenty years separating the two, the United Nations had held other large conferences: on human settlements in 1976; on desertification in 1977; and on new and renewable sources of energy in 1981. The major conference, covering these topics and more, was the UN Conference on Environment and Development (UNCED) held in Rio de Janeiro in June 1992 and nicknamed the 'Rio Summit' or the 'Earth Summit'.

Attended by leaders from 178 countries, UNCED was the largest summit meeting ever held. It concluded with a number of agreements. The Convention on Protecting Species and Habitats (the so-called Biodiversity Convention) was signed on behalf of 167 countries and the Framework Convention on Climate Change was also accepted by more than 150 countries. It was also agreed that the Rio Declaration on Sustainable Development, signed at the Conference, would be passed together with Agenda 21, the outline of a programme for action, to the UN Sustainable Development Commission, a body the General Assembly was asked to authorize.

Not everything was agreed. Decisions on forestry, desertification, and fish stock management were postponed for a later conference. Nor did all subsequent discussions run smoothly. Nevertheless, UNCED was regarded as a considerable success and some governments produced documents relating what had been agreed in Rio to their own countries and policies. The British government published its *Sustainable Development Strategy*.

It is never likely to be easy to persuade national governments to cooperate in matters that affect their perception of sovereignty, which is generally taken to mean their inalienable right to assert the interests of their own peoples. Yet much was achieved between about 1970, when the existence of a complex of problems that could be addressed effectively only at a global level was first widely recognized, and 1992. Virtually all governments had come to accept the need for international collaboration and environmental legislation. Problems identified at the global level were being discussed and made the subjects of intensive scientific research. Sustainable development, whatever it might mean in practice, was held to be the necessary route to future environmental stability. It would be no exaggeration to say that during this period, from 1970 to 1992, the attitude of world leaders changed radically.

62 Pollution control

All the strategies for conserving the environment called for pollution to be reduced, but achieving any significant improvement meant that politicians and the public had to address the economic issues raised by pollution control. In a market economy, goods and services are produced in response to consumer demand, which in most cases is sensitive to price. If prices rise, demand falls, and where alternative products or services are available at different prices, consumers will tend to prefer the cheaper. This strongly encourages producers to minimize their costs in order to keep prices as low as possible and, therefore, only those costs actually incurred in the course of production and distribution, such as materials, fuel, wages, administration, transport, and marketing, were counted in the retail price. These are the internal costs.

Every manufacturing process generates waste and by-products with no commercial value, and every product eventually wears out and is thrown away. Some products, such as detergents and the propellants used in aerosol cans, are thrown away immediately, in the course of their ordinary use. Others, such as coal, generate and release by-products in the course of their ordinary use. Wastes and by-products

were traditionally released into the environment at every stage in the production and use of goods and services. If not always free, disposal was cheap.

What the environmental debate revealed, however, was that such disposal does incur costs. Most obviously, water polluted by industrial or domestic discharges may have to be purified for return to the public supply, and this increases the cost of that supply. Less obviously, in the sense that it is more difficult to quantify, polluted air may harm the health of some people, requiring them to seek medical treatment that must be paid for, by the community at large or by themselves depending on the system of health care, quite apart from the cost they pay in terms of suffering. Such costs as these, and there are many, are borne either by the public as a whole or by individuals. They are not borne directly by the suppliers or consumers of the goods and services that gave rise to them. They are external costs.

In the jargon of economists, pollution control seeks to internalize these external costs. Where the costs arise in the course of production, they should be charged to the producer. This is the basis of the 'polluter pays' principle. Of course, this may increase production costs and, therefore, the price paid by the consumer, but this is considered fair. People who do not consume that particular product or service no longer contribute to the costs incurred through the disposal of its wastes and by-products.

Where the environmental costs arise from consumption, matters are rather more complicated, because in practice it is usually impossible to charge for the disposal of individual items. One alternative is to encourage, or in some cases compel, the consumer to dispose of wastes in ways that minimize the final disposal cost or maximize opportunities for recycling. This is the reasoning behind bottle, paper, aluminium can, and clothing banks, and the system in some countries, such as Germany, that requires householders to sort their domestic refuse into separate containers. A more radical approach is to require the producer to assume responsibility for, and bear the cost of, final disposal of the product. At the end of its life, for example, a car might be returned to the factory that made it.

Reducing sulphur emissions

Coal-burning is a major source of sulphur dioxide emissions. These can be reduced by flue-gas desulphurization, or by burning the coal in a fluidized bed.

Flue-gas desulphurization works by reacting gaseous sulphur dioxide (SO₂) with lime (calcium hydroxide, Ca(OH)₂) to produce calcium sulphate (CaSO₄). The flue gas is passed through a lime bath and the insoluble CaSO₄ is precipitated. The process is efficient, but generates large amounts of waste CaSO₄ and requires a large supply of lime. This is obtained by quarrying and then kilning (heating) limestone, a process that drives off carbon dioxide (CaCO₃ + heat \rightarrow CaO + CO₂ \uparrow).

In a fluidized bed, powdered coal is mixed with powdered limestone and the mixture burned in a chamber through which air is forced under pressure from below, making the mixture behave like a fluid (hence the name). The forced circulation of air and separation of particles ensure more efficient combustion than in a conventional furnace, and at a lower temperature. Efficient combustion reduces emissions of unburned hydrocarbons, the lower temperature reduces the oxidation of nitrogen to nitrogen oxides, and sulphur dioxide reacts with the limestone. SO₂ emissions are reduced by about 90 per cent.

Before any system of pollution control can be implemented, its costs must be quantified, and this is not straightforward. The cost of pollution abatement increases sharply as emissions fall, imposing an upper limit on the improvement that can be achieved at a price the public is willing to pay (RAVEN *ET AL.*, 1993, pp. 116–121). Just how much people will pay depends on a comparison between the cost of the pollution and the cost of reducing it. Pollution costs can be calculated, for example as the cost of health care and lost working time attributable to pollution, although this is difficult and usually controversial, because it relies on epidemiological studies that yield probabilities, not certainties, and are open to varying statistical interpretations (TAUBES, 1995). Nor does pollution exact the same price in all places. Smoke from a particular factory causes much less harm in the countryside, far from any other factory, than it would in a city where it mingled with smoke from many other factories. Is it just, therefore, to require all factories to observe the same emission limits regardless of the actual harm they cause? It can be argued that similar costs must be imposed on all factories to prevent some enjoying a commercial advantage over their rivals. It can also be argued that lower costs in certain places would encourage the more even distribution of industry, favouring regions that are otherwise economically disadvantaged.

In the real world, pollution abatement proceeds as a series of compromises between the clean environment the public demands, the degree of improvement industries are technologically capable of achieving, and the overall effect on prices and national economies. It is supported by national and international legislation. This explains in detail what is expected and protects responsible producers from those prepared to undercut prices by ignoring environmental considerations. There is now a vast amount of environmental legislation, and exporting companies must observe the laws obtaining in all the countries to which their products are sent.

Industry has learned to accept environmental constraints and it would be wrong to suppose it necessarily hostile. After all, factory owners and managers breathe the same air, drink the same water, and visit the same countryside as everyone else. They share the general desire for environmental improvement, and many members of the public urging that improvement are also their employees.

Complacency is the vice guaranteed sooner or later to lead an industrialist into bankruptcy. Industrialists are opportunists and soon began to realize that constraints could be turned to advantage and costs into profits. Markets were found for some of the substances recovered from waste streams and in future we may expect some economic surprises. Agricultural crop plants require sulphur as an essential nutrient, for example. Until now they have received an adequate supply in the form of sulphur dioxide dissolved in rain. The sulphur dioxide is an industrial emission that contributes to acid rain. As it is recovered from exhaust gases to reduce acid rain damage, crop plants will be deprived, so perhaps the recovered sulphur can be sold to farmers as fertilizer. Acid rain would be reduced to some extent and farmers would have to pay for what they were used to receiving free.

More immediately, pollution abatement has become an industry in its own right. The manufacture, installation, and maintenance of the necessary equipment is a specialized and profitable enterprise. Large companies must provide themselves with laboratories to determine the environmental effects of their products, and those laboratories must be equipped and staffed. Many are much better equipped than university laboratories. This need has made work for the manufacturers of laboratory equipment and consumable supplies, and provided employment for scientists and laboratory technicians.

Removing pollutants once they have been generated is, at best, an interim measure and only some of the recovered substances have any commercial value. The search, therefore, is for technologies that generate fewer pollutants in the first place. Such technologies would be more easily sustainable. They would recover, recycle, or reuse materials as part of their primary process, substitute process

materials to take account of their environmental effect (such as using water-based rather than solventbased paints), and in some cases modify the product itself (HOOPER AND GIBBS, 1995). The obvious sense of this is recognized by governments and intergovernmental bodies such as the Organization for Economic Cooperation and Development (OECD). Since the goal of environmental improvement is socially popular and promises reductions in public expenditure, some governments are now providing practical support for environmental technologies (CLEMENT, 1995). As Figure 6.11 shows for the European Union, there is considerable variation in expenditure from one country to another, although the figure makes no allowance for the relative sizes of national economies.

The concept of 'cleaner technology' emerged in the late 1970s and led in some countries to a reduction in pollution and consumption of raw materials that was clearly discernible a few years later. Although supported by governments, industries paid for much of the investment themselves, as Figure 6.12 shows. Amounts vary, but in countries with the most stringent environmental regulations annual expenditure on pollution control is about 1.5 per cent of GNP, of which industry pays around 25 per cent, or 0.4 per cent of GNP (TOLBA AND EL-KHOLY, 1992, p. 358).

Pollution control may be profitable for those selling it and cleaner technologies may improve industrial profitability once they are installed, but those benefits cannot be obtained unless there is capital available to invest in them and a highly trained workforce to install and operate them. For this reason, the environmental gains have been most marked in the wealthy, industrialized



Figure 6.11 Government assistance for environmental technologies In the EU1988–90 After Clement, Keith. 1995. 'Investing in Europe: Government support for environmental technology', Greener Management International, January, p. 45



Figure 6.12 Private investment In pollution control during the 1970s and 1980s (1980 prices) Source: Tolba, Mostafa K. and El-Kholy, Osama A. 1992. The World Environment 1972–1992. Chapman and Hall, London, on behalf of UNEP

countries. Poor countries simply cannot afford to abandon existing industrial plant while it remains capable of producing goods, albeit inefficiently, nor to install equipment to recover pollutants.

Carbon dioxide emissions provide one way to measure differences between countries. Older industrial and power generation plants burn fossil fuels as their primary source of energy and in poorer countries fossil fuels also provide most domestic heating and cooking. Modern plant, both industrial and domestic, uses energy more efficiently, so it consumes less fuel for each unit of energy delivered, and it is more likely to rely on alternatives to fossil fuels, most notably nuclear power for electricity generation. The more carbon dioxide that is released for each unit of national income, the poorer and more technologically backward the country. As Figure 6.13 shows clearly, emissions and prosperity follow one another closely. China produces seven times more carbon dioxide than the United States for each US dollar of its income.

This situation is unsatisfactory and China began to do something about as long ago as 1979. By 1987 a system of pollution charges had been extended to the entire country. Since 1988 efforts have been directed at improving the policing of the system. This begins by setting standards for a range of pollutants. There are more than a hundred standards for discharges into water, atmospheric emissions, waste disposal, and noise. Those who exceed them must pay a charge based on category of pollution. After three years, continued failure to comply results in a 5 per cent annual increase in the charge, and a double charge for any new enterprise exceeding the standards that was built after the legislation was passed. A delay of more than twenty days in paying a charge incurs a penalty of 0.1 per cent per day. Money raised by the charges is invested in pollution control and, although the charges are lower than the cost of installing control equipment, so that many managers are content to pay them and carry on polluting, they have led to environmental improvements in the most heavily polluted cities and regions and provided employment for more than 40000 people (POTIER, 1995).

Nevertheless, pollution remains severe. The area affected by acid rain increased from 18 per cent of the total land area in 1985 to 40 per cent in 1998, due to dependence on coal during a period of rapid economic growth. Scientists calculated that unless emissions from Chinese coal-fired plants



Figure 6.13 Carbon dioxide emissions in 1988 (kg per US\$ of national income) Source: Nowicki, Maciej. 1992. Environment in Poland. Ministry of Environmental Protection, Natural Resources and Forestry, Warsaw

were reduced, by 2020 deposited acid would overwhelm the ability of soils to cope over a large area, on a scale equivalent to or exceeding that in the 'black triangle' of central Europe. It would cost more than \$23 billion per year for 20 years, about 2 per cent of China's gross domestic product, to remedy the situation. Scrubbers to remove sulphur dioxide would have to be installed on all new and all major existing smokestacks and power plants, and greater energy efficiency and a switch to less polluting fuels would have to be encouraged (HOLMES, 1999). Coal accounts for 75 per cent of total Chinese energy consumption and about 22 per cent of Chinese homes use uncleaned coal for cooking and heating. As well as sulphur dioxide, domestic cooking fires emit arsenic, fluorine, lead, and mercury.

There has been great concern over levels of pollution in the industrialized regions of Eastern Europe. These, too, result from old, inefficient industrial plant and over-reliance on low-quality coal as a primary energy source. The governments of those countries are no less determined than others to remedy the problem. Poland, where carbon dioxide emissions are relatively greater than those in Russia, has implemented a programme to reduce its economic reliance on heavy industry, move from coal to domestic and imported natural gas as a principal fuel, and modernize its old power stations. At the same time, it is encouraging energy conservation in industry, transport, and domestic heating and cooking (NOWICKI, 1992, p. 6).

The impetus arising from the environmental concerns of the 1960s and 1970s led to the conservation strategies of the 1980s and, from them, to the concept of 'sustainability'. This is now being translated

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into everyday industrial practice first in the industrialized countries but increasingly in the less industrialized and newly industrialized countries. Improvements are already becoming evident and, provided the momentum is maintained, more will appear in years to come.

63 Hazardous waste

Wastes are ordinarily disposed of in landfill sites or by incineration. These methods are not satisfactory for certain types of waste, however. Under British law, the Control of Pollution Act 1974 defines wastes and regulates their disposal according to the risk this presents.

Controlled wastes, categorized as household, commercial, or industrial, must be collected and disposed of in such a way that they cannot cause pollution. Agricultural wastes, explosives, and wastes from mines and quarries are not defined as controlled wastes.

Special wastes include prescription drugs, substances with a flash point below 21°C, and other materials that present disposal difficulties. Wastes that are poisonous, but do not fall within the definitions of special waste are classed, rather loosely, as toxic wastes.

Hazardous wastes are also defined rather loosely. They include substances similar to special wastes, but listed under the Transfrontier Shipment of Hazardous Wastes Regulations 1988. Difficult wastes include all special wastes together with certain metallic wastes and wastes that are physically difficult to handle. The final category covers clinical wastes (BMA, 1991, pp. 22–24).

All the definitions are vague, but they do impose on all manufacturers a legally binding obligation to state the precise chemical composition of wastes they discharge and to list any toxic substances they contain. The best disposal method then depends on the nature of the waste. Some toxic substances can be made safe by diluting them, for example, but others must remain completely isolated from the environment (MELLANBY, 1992, pp. 55–67 and Appendix 3).

The imposition of more stringent controls on the disposal of wastes has led to the emergence of companies specializing in waste disposal. They have the expertise to categorize waste accurately and the facilities to render it safe. Because one disposal facility accepts wastes from many sources, this greatly simplifies the policing of the regulations. From lime to time 'cowboy' operators seek to undercut the prices of legitimate companies, but any pollution they cause can be traced back to them fairly easily.

Traffic in waste

As industrialized countries tightened the regulations controlling the disposal of wastes that could harm human health or pollute the environment, specialist companies emerged to handle them. Specialist disposal is much more expensive than dumping wastes on land or discharging them into water, however, and an alternative method also emerged. Companies collected wastes and shipped them overseas. They went either to countries with adequate disposal facilities and underused capacity, or to developing countries that lacked proper means of disposal, but welcomed the foreign-currency payments they received for accepting them. Sometimes the wastes arrived unlabelled or incorrectly labelled and caused serious harm locally. The international trade in toxic wastes became a matter of great concern and on March 22, 1989, the Convention on Transboundary Movements of Hazardous Waste was adopted at a conference held in Basel, Switzerland, under the auspices of the UN Environment Programme. Known as the Basel Convention, it was signed by 34 countries, with general endorsement from an additional 105. It established the right of every country to refuse to accept cargoes of hazardous wastes, established rules for the notification of planned shipments, and obliged the governments of originating countries to ensure that the recipient countries have adequate storage and treatment facilities. Wastes that are dumped illegally can be returned to their country of origin.

On March 25, 1994, signatories to the Basel Convention agreed that from the end of 1997 it would be illegal to export wastes to less developed countries for recycling, although the EU planned to continue to export wastes that presented no risk. At a further meeting, held in Kuching, Malaysia, in February 1998, more than 300 officials from 117 countries agreed on a list of materials defined as 'hazardous', and on a list of countries that were permitted to trade toxic waste among themselves.

64 Transnational pollution

Drifting air masses, continental rivers, and ocean currents are no respecters of national boundaries contrived by politicians and generals. They move where physical forces take them, and if they carry a load of pollutants those travel with them. Consequently, there is a limit to the pollution abatement that individual nation-states can achieve in isolation.

Free trade imposes a further constraint. Consider the case of two widely separated countries; call them A and B. Country A, heavily industrialized, suffers severe pollution of its air and fresh water, and its government, responding to pressure from a concerned citizenry, enacts legislation to protect the environment within its borders. This increases manufacturing costs. Country B, on the other hand, is either just industrializing and experiences little pollution or is prepared to tolerate such pollution as it has. Following the legislation in country A, its manufacturing costs are lower and country A is therefore presented as a tempting market it can penetrate with little difficulty. Country A is now in a difficult position. If it does nothing, its trading account will deteriorate and so will its overall economy. In the end, its citizens will suffer. If it seeks to protect its domestic manufactures by imposing tariffs and duties it risks distorting trade patterns and triggering reprisals.

The conclusion in 1994 of the Uruguay Round of negotiations on the General Agreement on Tariffs and Trade (GATT) represented a major liberalization of world trade and the replacement of GATT itself by a new body, the World Trade Organization (WTO). Some environmentalists feared it might lead to the relocation of industries from regions with stringent environmental legislation to those with lax controls, or that controls in the present industrialized countries might be relaxed. Others feared that economic development would be inhibited in the less industrialized countries through an insistence by countries with strong environmental regulations that similar regulations be imposed on the manufacture of goods they imported. These dangers have been recognized and ways are being sought to address them (VON FELBERT, 1995).

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It is in the interest of all countries that, so far as possible, environmental policies are coordinated. In practice, this is what has been happening since the 1972 Stockholm Conference and considerable progress has been made.

Acid rain may have been the first issue demanding international agreement. The phenomenon had been known for more than a century, and the monitoring of atmospheric acidity over northern and western Europe began in the 1950s (ALLABY, 1989, pp. 106-107), but it was in the 1970s that it was observed over Scandinavia and north-eastern North America. North-western Europe, eastern North America, and eastern China are still the regions most seriously affected but, as Figure 6.14 illustrates, several other parts of the world are potentially at risk. Because the acid derives in part from industrial atmospheric emissions that often travel long distances carrying sulphur dioxide and nitrogen oxides, its effects can be reduced only if nations collaborate. The fact of such transport was established by a case study Sweden presented to the Stockholm Conference in 1972, which led to larger study programmes, from 1972 to 1977 sponsored by the OECD, and starting in 1978 sponsored by the Economic Council for Europe (ECE). The ECE Convention on Long-Range Transboundary Air Pollution (www.unece.org/env/lrtap) was signed by 34 countries in 1979, a conference on the matter was held in 1982 in Stockholm, and in 1985 21 of the countries that signed the ECE Convention agreed the '30 per cent Protocol'. This committed them to reducing sulphur emissions by at least 30 per cent of their 1983 levels by 1993 at the latest. A further Protocol to the Convention, signed by 27 countries in 1988, called for emissions of nitrogen oxides to be no higher than their 1987 levels by the end of 1994 (TOLBA AND EL-KHOLY, 1992, p. 25).

The Convention has proved highly successful. Between 1980 and 1999 European emissions of sulphur were reduced by half, those of nitrogen oxides by 16 per cent, of volatile organic compounds by 20 per cent, and of ammonia by 18 per cent. The reductions have not been uniform, however. Some countries achieved much more than others. A further protocol was added to the Convention in November 1999. This dealt with acidification, ground-level ozone, and the eutrophication of surface waters.

Acid rain, more correctly called 'acid deposition' because airborne acid can travel as mist, fog, snow, and in dry air, as well as in rain, affects trees, soils, and surface water. The processes by which it does so are complex and often indirect. It has often been stated, for example, that airborne sulphate dissolves in cloud droplets to form sulphuric acid. While this is true, the resulting acid is often too dilute to harm plants directly. The damage it causes arises from chemical reactions in certain soils. The extent of the effect on forests is also difficult to determine and has sometimes been overstated (ALLABY, 1999, pp. 164–169). Research into the many facets of the problem has continued over many years and the full account of its nature and extent has at last been assembled (MACKENZIE AND EL-ASHRY, 1989).

Signing an agreement does not make the problem vanish, of course. The agreement must be ratified through national parliaments or assemblies and then implemented. This may prove more difficult than was predicted at the time of signing, either technically or because of fluctuations in the economic fortunes of the signatory states or the political fortunes of their governments. Even if the agreement is implemented, it may prove insufficient. Nevertheless, no improvement is possible without international agreement, so an agreement's conclusion and signature is an essential first step toward amelioration, even though acid rain continues to cause concern.

A similar, but in some ways even more intractable, problem affects what UNEP calls 'regional seas'. These are seas which are landlocked, or almost so, such as the Mediterranean and Red Seas, and seas bordering continents that are vulnerable to pollutants reaching them from the land. The first to be debated was the Mediterranean and it provides an excellent, if extreme, illustration of the difficulties involved.





As Figure 6.15 shows, the Mediterranean and Aegean are bordered by Spain, Gibraltar, France, Monaco, Italy, Croatia, Yugoslavia, Greece, Macedonia, Turkey, Cyprus, Syria, Lebanon, Israel, Egypt, Libya, Malta, Tunisia, Algeria, and Morocco. The countries to the north are industrialized, those to the south not, the cultures are Christian (both Eastern and Western), Jewish, and Islamic, and relations were less than friendly between Greece and Turkey at the time of the negotiations. Oil tankers sailing between the Gulf and Europe and North America pass through the Suez Canal and cross the Mediterranean, and many of them used to wash out their tanks in the Mediterranean as they returned empty to collect a fresh cargo. In addition, the Mediterranean system of inter-linked basins receives industrial discharges carried by the Ebro, Rhône, Po, Danube, Dnieper, Don, and Nile, as well as many smaller rivers.

Despite the apparent hopelessness of the task (at least Yugoslavia was still united and at peace at the time), meetings of the nations bordering the Mediterranean were held under UNEP auspices. These led to the adoption, at Barcelona in February 1976, of the Convention for the Protection of the Mediterranean Sea Against Pollution (the Barcelona Convention). It dealt with oil pollution and a range of industrial discharges, although it did not specify their sources. The Convention included an Action Plan setting out specific means for achieving its objectives.

This was the first agreement in what became the Regional Seas Programme. It has produced agreements to reduce pollution in such enclosed marine areas as the Red Sea and the waters south of Kuwait, and the Black Sea (bordered by Bulgaria, Romania, Ukraine, Russia, Georgia, and Turkey) was brought into the area covered by the Barcelona Convention (see Figure 6.15). In all, seven conventions have been agreed since the Barcelona Convention, covering Kuwait (1978), West and Central Africa (1981), the South-East Pacific (1981), the Red Sea and Gulf of Aden (1982), the Wider Caribbean (1983), Eastern Africa (1985), and the South Pacific (1986). The next to be agreed will cover the South Asian Seas, East Asian Seas, and North-West Pacific. Most of these agreements also involve the conservation and management of resources, such as fish stocks (TOLBA AND EL-KHOLY, 1992, pp. 775–777). Figure 6.16 shows the areas included in the Regional Seas Programme.

Countries bordering them have also concluded agreements independently of UNEP to protect particular seas. The Helsinki Convention, signed in 1980, covers the Baltic. In the North Sea, water enters through the Strait of Dover and is carried by the tidal system around the coasts of bordering countries, collecting river discharges as it goes, so coastlines are especially vulnerable, the German Bight being the most seriously affected area. Pollution of the North Sea is covered by the Oslo Convention, signed in 1972 and dealing with discharges from ships at sea, and the Paris Convention of 1974, dealing with pollution from land sources (CLARK, 1992, pp. 126–147). Rivers that cross or mark international borders have also been the subjects of agreements to reduce pollution.

As well as brokering international agreements, UNEP is responsible for coordinating the monitoring networks without which protection of the global environment would falter for want of data. These data are obtained from surface stations distributed throughout the world.

Their observations are augmented by satellite data. SPOT (Système Probatoire d'Observation de la Terre), launched in 1986, has a monochrome resolution of 10 m and provides information for farmers, geologists, and land-use planners. ERS-1 monitors ice patterns and surface temperatures. ERS-2 does the same, but also monitors ozone levels. JERS-1 gathers a wide range of data and Radarsat, launched in 1995, measures the Earth's surface. Several more satellites are planned. ADEOS, to be launched in 1996, will study atmospheric chemistry and collect land and sea data. Meteor 3M-1, to be launched in 1998, will study atmospheric aerosols and chemical compounds. In 1999, ADEOS II will begin studying surface wind speeds and directions over the oceans. Th







United States has a continuing programme of eight satellite launches between 1998 and 2003 and launch of the space station in 2001, which will considerably increase the flow of environmental data returned to Earth (LAWLER, 1995).

Data are processed and distributed through several systems. The Global Observing System (GOS) specializes in meteorological data. It is coordinated by the World Meteorological Organization (WMO) and operated by WMO member states. The Global Environmental Monitoring System (GEMS), established by UNEP, covers 142 countries and handles data pertaining to atmosphere, climate, pollution, and renewable resources. GEMS has several component systems. The Human Exposure Assessment Locations Programme (HEALS), for example, established in 1984 and run by the World Health Organization (WHO) in collaboration with UNEP, monitors human exposure to a number of pollutants (TOLBA AND EL-KHOLY, 1992, pp. 612–618).

Transnational pollution is not a recent phenomenon. Acid rain, first reported more than a century ago, must already have been causing damage for many decades and in those days of intensive heavy industry deriving its energy from coal-burning, it would be surprising if acid pollutants had not been transported from Britain across the North Sea by the generally westward movement of air masses, or from the industrial cities of the north-eastern United States and eastern Canada to adjacent rural areas. Similarly, industrial and domestic wastes were discharged into rivers and from there into the sea long before the means existed to measure the scale on which pollutants from one country were affecting the shores of others.

What has changed is not so much the character of transnational pollution as our increasing ability to measure and track it, and to observe and quantify its effects. It is through advances in technological sensitivity and scientific understanding that we are able to determine when and where pollution originates and the degree of its severity. These same advances allow us to devise ways of minimizing the harm it causes.

With the exception of greenhouses gases, the discharge of which may lead to changes in the global climate, most pollution affects local areas or regions. Local, regional or global, however, it can be ameliorated only through international cooperation. Recognition of this fact has compelled governments, often reluctantly, to modify their concepts of national sovereignty by admitting a wider duty to impose constraints on domestic activities for the benefit of citizens and environments beyond their borders. In this century we have learned that truly we all inhabit a single planet. As Barbara Ward and René Dubos wrote in their introduction to *Only One Earth*, the background book to the 1972 Stockholm Conference: 'As we enter the global phase of human evolution it becomes obvious that each man has two countries, his own and Planet Earth.'

The perceived need for international collaboration to protect and enhance the environment we all share offers the hope that such collaboration may expand into other areas of concern and that we may learn at last how to live in closer harmony with one another as well as with our planet.

End of chapter summary

Concern for the natural environment is far from new. Attempts to conserve resources such as forests and to reduce air pollution date from medieval times. In the course of this century, however, those attempts have broadened and, perhaps for the first time in history, they promise to be effective.

The most important change in our attitude to the environment comes from our recognition of its global extent. We have learned to appreciate that events happening here and now can produce environmental consequences far removed in place and time. This is novel. In previous centuries

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thoughtful people often expressed concern about the environment, but it was always the local environment they sought to improve, because they lacked the technological means to compile a picture that encompassed an entire country, region, or continent simultaneously, far less the entire world. With comprehensive satellite monitoring and electronic means of communication we now have that ability. Every point on the surface of our planet is under constant surveillance. It has given us the concept of 'Spaceship Earth'.

Our newly acquired broad view is accompanied by a deeper technical understanding of the way the environment works. This understanding is very far from complete, but it is improving rapidly and already it allows practical steps to be taken to protect species, habitats, landscapes, and human health that have a good chance of succeeding. Zoos, once menageries for the amusement of the rich and then potential breeding stations for the production of new farm animals, are now dedicated to the conservation of rare and endangered species. Agricultural improvements have greatly increased crop yields in Europe and North America, so less land is needed for farming. This makes it practicable to set land aside for non-agricultural purposes, such as recreation and wildlife conservation. So-called 'industrial' farming may remove much of the natural flora and fauna from the farmed area, but it also frees large areas elsewhere.

It is not only our comprehension of the environment that has assumed a global dimension. So have the economies and political structures of nations. International institutions now exist to resolve a wide range of issues by negotiation and agreement. Once the institutional framework had been set in place, environmental matters affecting more than one nation were fitted into it. The creation of the United Nations, first mooted in 1942 and finally achieved in 1945, made it possible to form the United Nations Environment Programme (UNEP) in 1973. UNEP and other UN agencies have been instrumental in nurturing many of the international environmental treaties and conventions that have been implemented over the last few decades.

Despite the fears of some environmentalist scaremongers, we have good reason to be optimistic about the future. It is simply not true that the world is irredeemably damaged. The well documented fact that in almost every corner of the world people are healthier and living longer than they did a generation ago gives the lie to the idea that the human environment is becoming more hostile. There are environmental problems, areas that have been severely damaged, and valuable habitats that are being lost and their species threatened with extinction. But as our knowledge expands and informs our political will to protect, restore, and reconstruct, we may hope and expect that in the years to come the condition of the global environment will improve.

End of chapter points for discussion

How did zoos and botanic gardens originate? What is the best way to control farm pests? Do world conservation strategies have any effect? What is the precautionary principle and what are its advantages and disadvantages?

See also

Human populations and demographic change (section 54) Genetic engineering (section 55) Zoos, nature reserves, wilderness (section 57)

Further reading

- *The DDT Story.* Kenneth Mellanby. 1992. British Crop Protection Council, Farnham. Short and simple to read, this book tells the full history of the world's most notorious insecticide and is written by a scientist closely involved in monitoring its environmental effects.
- *North-South: A Programme for Survival.* The Independent Commission on International Development Issues. 1980. Pan Books, London. A detailed analysis of the economic and environmental situation facing the world.
- *Our Common Future.* The World Commission on Environment and Development. 1987. Oxford University Press, Oxford. The famous Brundtland Report, which provided background material for the 1992 Rio Conference.
- *Silent Spring.* Rachel Carson. 1963. Hamish Hamilton, London. Still in print, this is the book that first aroused public concern about the condition of the environment.

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End of book summary

The concept of the environmental sciences is still evolving. Like the life and Earth sciences, it comprises elements taken from many disciplines. It differs from the other broad scientific groupings in its political and social implications and this means it attracts much more attention from the public.

Public concern about the condition of the natural environment has stimulated the development of a large, sophisticated, and politically powerful environmentalist movement. Its leaders have their own ideas about the way the environment should be managed and the social and economic reforms that, in their view, are necessary if this is to be achieved. Their ideology is essentially moral and not necessarily dependent upon a scientific appraisal of the issues that engage them.

This book deals with environmental science, not with environmental philosophy or ideology. Although the two are distinct, they remain linked, however. An understanding of the science will inform your opinions and help you to distinguish between fact and fancy, to allot priorities, and to judge the likely effectiveness of particular courses of action.

You may not count yourself an environmentalist, but if you are to enter any profession that requires you to alter any aspect of the natural environment in any way at all you will need a basic grounding in environmental science. It will be your responsibility either to estimate the likely environmental consequences of the change you propose or to evaluate critically the estimation made by someone else. To do that you will need to understand the science.

Basics of Environmental Science provides no more than an introduction to a truly vast topic. Its purpose is to give you a broad idea of what environmental science entails and to whet your appetite so you may be encouraged to pursue your studies further.

In the course of the six chapters into which the book is divided you will have encountered the environmental dimension of most of the disciplines that comprise the environmental sciences. You will also have been introduced to many of the key concepts. Although you need not read them in order, the chapters follow a logical sequence, from Earth sciences to physical resources, from biosphere to biological resources, and finally to environmental management.

Scientists do not and cannot provide certainty. Science is based on scepticism and a proper response to any scientific assertion is to challenge it. In this ruthless selection process only the most robust explanations survive. Consequently, scientific discoveries and ideas are necessarily somewhat provisional. They may be modified or replaced in the light of new knowledge. This is the way science works, but it is profoundly unsatisfactory to those seeking reassurance or absolute answers that will remain true throughout eternity. Not surprisingly, therefore, many scientific issues are controversial.

You have been introduced to a few of the controversies. Is global warming happening? If so, is it due to our emissions of greenhouse gases or to some other cause, such as changes in the solar output? If land is set aside for conservation, should it be in the form of a single block or divided into many smaller blocks linked by pathways? Given that not all areas of ecological value can be protected from development, how shall we choose which to protect and which to abandon? Is modern intensive farming good or bad for wildlife?

As an environmental scientist you will join the search for answers to these questions and many others like them. Even if you never find an answer, the search will reveal new knowledge that will add to our understanding of the world in which we live. The search is valuable, even if it proves fruitless. That is science.

Good luck.



adaptation The process by which species adapt evolutionarily (i.e. acquire adaptedness).

adaptedness The condition of a species that is adapted to the conditions under which it lives.

adiabatic (*adj.*) Without exchanging energy with the surrounding medium. Applied to a change in air temperature occurring solely as a consequence of the air rising (and cooling) or descending (and warming).

aeolian Wind-blown.

aeroplankton Spores and other microscopic organic particles and organisms that drift in the air because they weigh so little that they fall only slowly and are likely to be carried aloft again by rising air currents before settling on a surface.

aerosol A colloid, in which particles are dispersed in a gas, usually air. Because of their small size $(0.01-10 \ \mu m)$, airborne aerosols fall very slowly.

aggressive mimicry The resemblance of a predatory or parasitic species to its prey or host.

albedo A measure of the amount of radiation a non-luminous body reflects.

Allen's rule A rule, proposed by J.A.Allen, stating that projecting parts of the body of mammals (ears, muzzle, and tail) tend to be larger in animals living in warm climates than in closely related animals living in cold climates.

allogenic (adj.) Applied to an ecological succession driven by abiotic environmental changes.

alluvial Formed from sediment deposited by a river.

amino acid One of the constituent units of a protein, comprising an amino group (NH_2) and carboxyl group (COOH) both attached to the same carbon atom. Of more than 80 naturally occurring amino acids, about 20 are commonly found in proteins.

anion A negatively charged ion.

aphelion The point at which an orbiting body is furthest from the body it orbits.

aquifer A body of permeable material below ground through which water flows.

autogenic (*adj.*) Applied to an ecological succession driven by environmental changes induced by vegetation.

autotroph An organism that can synthesize the organic compounds it needs for nourishment from simple, inorganic molecules.

Batesian mimicry The close resemblance between a species that is palatable to predators and an unrelated species that is unpalatable, leading predators to avoid both. It was first observed by H.W.Bates.

Bergmann's rule A rule, proposed by C.Bergmann, stating that animals living in cold regions are larger than closely related animals living in warm regions.

biodiversity An abbreviation of 'biological diversity' and usually taken to mean the total number of species presently living on Earth.

biogeochemical cycles The transport of elements between rock, water, air, and living organisms in an approximately circular fashion that periodically returns them to each stage.

biological control The control of pest populations without using chemical pesticides, most commonly by stimulating parasites and predators of the pest.

biological oxygen demand (BOD, biochemical oxygen demand) A measure of the pollution of water by organic matter (e.g. sewage), calculated by measuring the weight (in milligrams) of oxygen utilized, and so removed from a sample of water, by microorganisms during 5 days at a constant temperature of 20°C.

biomagnification (bioaccumulation) The accumulation in the body of repeated small doses of an ingested substance until it reaches a sufficient concentration to produce physiological effects.

biomass The total mass of all living organisms within a defined area, or at a particular trophic level within that area.

black body A body that absorbs all the radiation falling upon it and reradiates it at a wavelength determined by its temperature.

'black smoker' A hydrothermal vent on the ocean floor emitting fluids containing iron, manganese, and copper. These tend to be black and resemble smoke. Vent fluids containing zinc and arsenic are usually white, and known as 'white smokers'.

'blue baby' syndrome See methaemoglobinaemia.

carbon ⁻14 (¹⁴C) A radioactive isotope of carbon with a half-life of 5730±30 years.

carbonation A chemical reaction between a compound and carbonic acid (H_2CO_3) that forms soluble bicarbonates.

carrying capacity The maximum population a specified environment can support over a prolonged period without degrading the environment.

cation A positively charged ion.

chromosome A thread of DNA and organic compounds found in the nuclei of all living plant and animal cells each species has a typical number (e.g. 46 in humans). Chromosomes consist of two paired strands. When cells divide, the chromosome strands separate, each daughter cell receiving one strand (called a chromatid). In body (somatic) cells the complementary chromatid is then synthesized.

climax The stable, enduring plant community that is the final result of a succession of communities (sere). The succession begins with the colonization of bare ground or water that sustains no plant life.

clone (n.) Two or more individuals that are genetically identical, or any one of those individuals, (v.) To produce a clone.

commensalism A relationship between two organisms of different species in which one (the commensal) benefits and the other (the host) is unaffected.

dewpoint The temperature at which atmospheric water vapour condenses or water evaporates.

disseminule A seed, spore, or fertilized egg that is broadcast (i.e. disseminated) randomly by an organism.

Dryas Two periods of cold climate, known as the Older Dryas and Younger Dryas, identified by the widespread occurrence of pollen from *Dryas octopetala* (mountain avens), an alpine plant. The Younger Dryas is dated at about 11000–10000 years ago.

ecliptic The great circle apparently traced by the Sun in relation to the 'fixed' stars in the course of a year. The plane of the ecliptic is the plane of the Earth-Moon orbit about the Sun. If the visible universe is imagined as a sphere (the 'celestial sphere') with the Earth at its centre, the ecliptic is at an angle to the equator of this sphere.

endozoochory The carrying of plant seeds by an animal inside its body.

epizoochory The carrying of plant seeds by an animal on the outside of its body (e.g. in its coat or feathers).

euphotic zone The upper region of a lake or sea within which light intensity is sufficient for photosynthesis.

eutrophic Over-enriched (with nutrients).

evolution The development of new species from pre-existing species, with no implication of a mechanism by which this occurs.

fluvial Pertaining to a river.

gamete An ova or sperm cell; these are the cells which fuse at fertilization and develop to form the new individual.

gene The basic unit of heredity, comprising a segment of DNA (or RNA in some viruses) of varying length that codes for a particular function or several related functions and occupies a fixed position on a chromosome.

gene bank An establishment where tissues, seeds, or genetic material are stored for purposes of conservation.

gene pool The total number of genes possessed by all those members of a sexually reproducing species or population that are capable of reproduction (i.e. in the reproductive phase of their lives).

genome The entire complement of genetic information carried by an individual in a single set of chromosomes.

genotype The genetic constitution of an organism.

geomorphology The scientific study of landforms and their relationship to underlying geologic structures.

Gloger's rule A rule, proposed by C.W.L.Gloger, stating that animals living in warm climates are more darkly coloured than closely related animals living in cold climates.

half-life The time taken for half an amount of a radioactive substance to decay.

heterotroph An organism that obtains the organic substances it needs for nourishment by consuming other organisms.

homoeostasis The tendency of a system to maintain its own equilibrium by resisting or adjusting to change.

homoiotherm An organism in which the internal body temperature varies only within narrow limits. Regulation may be achieved by internal (endothermic) or behavioural (ectothermic) mechanisms or a combination of both (as in humans, who sweat to cool themselves and shiver to warm themselves, but also wear variable amounts of clothing and light fires in winter).

humidity The amount of water vapour held in the air. The most commonly used measure is relative humidity, the amount of water vapour present in air as a proportion of the amount needed to saturate the air at the same temperature, and expressed as a percentage.

hydrosere A sere (ecological succession) that begins in water.

igneous (adj.) Applied to rocks formed directly by the cooling of material from the mantle.

inversion (temperature inversion) The situation in which air temperature remains constant, or rises, with increasing altitude within a layer of the atmosphere. Warm, rising air is trapped by an inversion, because it enters a region where the surrounding air is at the same temperature and density as itself. Thus inversions tend to trap pollutants carried upward in warm air.

ion An atom or molecule that has gained or lost one or more electrons and so possesses a net electric charge.

isostasy The flexing of the Earth's crust in response to local changes in its mass. If material is deposited at the surface, the crust beneath that material is depressed; surface erosion causes the crust to rise.

isotope An atom with a mass differing from other atoms of the same element because its nucleus contains more or fewer neutrons. The nucleus contains the same number of protons as other atoms of the element, so the atom is chemically identical.

lapse rate The rate at which air temperature changes with altitude. This depends on local conditions, especially humidity.

little Ice Age A period when average temperatures were lower than they are today throughout middle latitudes in the northern hemisphere. It lasted from about 1550 to 1860, with an especially severe episode in the early 1660s.

maximum sustainable yield (**MSY**) The crop that is equal to the number of individuals or biomass recruited to a population during the period (usually 1 year) for which it is calculated. Theoretically, this is the crop that can be harvested without depleting the population.

metamorphism The alteration of rock by exposure to changed temperature, pressure, or chemical environment, or some combination of these, most commonly leading to the dissolution and recrystallization of its mineral constituents.

methaemoglobinaemia ('blue baby' syndrome) A rare condition in young babies that occurs when nitrates ingested from food or water are converted to nitrites in their very acidic gastric environment (gastric acidity falls to levels at which this ceases to occur in infants older than about 6 months). The nitrites react with blood haemoglobin to form methaemoglobin, which forms a compound with oxygen that is more stable than oxyhaemoglobin and, therefore, gives up oxygen less readily to tissues requiring it. This produces blue skin coloration, due to oxygen deficiency in the blood, and consequent oxygen starvation of tissues. In extreme cases the condition can prove fatal.

microhabitat A defined part of a habitat within which a particular species or community is most likely to occur.

migration The mass movement of organisms from one place to another.

mitosis The process by which body (somatic) cells divide, each dividing call yielding two daughter cells. Although continuous, for convenience the process is described as comprising four distinct phases. (1) At prophase, the chromosomes contract, becoming visible under a microscope. Each separates into two parallel strands (called chromatids), and the nuclear membrane (enclosing the cell nucleus) disappears. (2) At metaphase, the pairs of chromatids move to a structure formed from protein fibres (called the spindle) and align themselves across its centre (called the equator). (3) At anaphase, the chromatid pairs separate and move to the opposite ends (called poles) of the spindle. (4) at telophase, the cell constricts across its centre, the spindle appratus disappears, the nuclear membrane re-forms, and the chromosomes extend to become long, fine filaments, not clearly visible under a microscope. Each daughter cell now contains a complete set of chromosomes. Between mitotic divisions (called interphase) each chromosome duplicates itself.

morph A particular form of an organism.

Müllerian mimicry The resemblance of one dangerous or poisonous species to another, leading predators to avoid all species of that appearance. It was first described by F.Müller.

mutation A change in the structure or amount of genetic material. Most mutations involve alterations within individual genes, but some comprise major restructuring of chromosomes or changes in the number of chromosomes in the cell nucleus. Mutations are inherited only if they occur in gametes or cells destined to become gametes.

mutualism A relationship between two organisms of different species from which both derive benefit.

nucleic acid Genetic material, occurring as DNA or RNA, that comprises strings of nucleotides.

nucleotide An organic molecule that forms the basic unit in nucleic acids and comprises a pentose sugar (ribose or deoxyribose), a phosphate group, and a purine or pyrimidine base.

oligotrophic Deficient in nutrients.

optimum sustainable yield (OSY) The crop that can be harvested without depleting the population. It is commonly calculated as half the carrying capacity.

oxygen-isotope analysis Examing the ratio of two isotopes of oxygen, ¹⁸O:¹⁶O, in a sample and inferring from the result information regarding the source or temperature of water or the water from which the sample (e.g. calcium carbonate or silica) was deposited. 'Light' water ($H_2^{16}O$) evaporates more readily than 'heavy' water ($H_2^{18}O$).

ozone layer A region of the stratosphere, at 20–25 km, where the concentration of ozone (O_3) is higher than elsewhere.

parasitism A relationship between two organisms of different species in which one (the parasite) lives inside or on the surface of the other (the host) and obtains food from it. Parasitism usually injures the host, although in some cases the effect is very slight.

pedogenesis The natural processes by which soil forms.

pedology The scientific study of soils.

perihelion The point at which an orbiting body is closest to the body it orbits.

permafrost Ground that is permanently frozen below the surface. It forms where temperatures below freezing have persisted through two consecutive winters and the intervening summer.

perturbation A disturbance to a system (e.g. the atmosphere, or an ecosystem) caused by something external to that system.

phenotype The observable appearance or characteristics of an organism.

phytoplankton Plankton comprising plants, most of them single-celled algae.

plankton Small organisms, including the juvenile stages of many larger organisms, that drift near the surface of water.

plate tectonics The theory that describes the Earth's crust as comprising a number of rigid sections which move in relation to one another. This movement causes ocean basins to open and close and continents to change their position and orientation.

poikilotherm (**exotherm**) An organism (e.g. a fish) in which body temperature varies according to that of its environment.

polymorphism The existence of different forms among the members of a species. These may be externally visible (e.g. the number of spots on the wings of ladybirds) or invisible (e.g. blood groups in humans) and may be transitory or permanent.

polyploidy The possession of one or more sets of chromosomes in addition to the two sets ordinarily found. It results from the replication of complete chromosome sets without a subsequent division of the cell nucleus.

purine One of the types of base found in nucleic acids. Adenine and guanine are purines and link only to pyramidines.

pyrimidine One of the types of base found in nucleic acids. Cytosine and thymine are the bases in DNA; in RNA uracil takes the place of thymine. Pyrimidines link only to purines.

radiocarbon dating A dating method based on the ratio of carbon-12 (¹²C) to carbon-14 (¹⁴C) present in a sample. Both isotopes occur in the atmosphere and are absorbed by living organisms. During life, therefore, the ¹²C:¹⁴C ratio in cells is identical to that in the atmosphere. After death, ¹⁴C decays and the ratio changes. By measuring the ratio in a sample and relating it to the known half-life of ¹⁴C, samples up to about 70000 years old can be dated. The ¹⁴C content of the atmosphere is not constant, but corrections are made for fluctuations over the last 8000 years by reference to the ¹⁴C content of tree rings in certain long-living species (e.g. bristlecone pine, *Pinus longaeva*).

radioisotope An isotope that is radioactive and can therefore be used to identify the location or track the movement of the element of which it is an isotope.

radiometric dating Calculation of the time that has elapsed since a rock or organic deposit formed by measuring the ratio of a radioisotope to its decay products or to a non-radioactive isotope and using the known half-life of the radioisotope to determine the time taken for an initial amount to decay to the concentration found in the sample.

residence time (removal time) The length of time a molecule or particle remains in a particular part of the environment (e.g. the air).

sequence (n.) The order in which bases occur in nucleic acid or amino acids in a protein, (v.) To identify and record that order.

seral stage One of the plant communities forming part of a sere (or succession).

sere The succession of distinct plant communities that follow one another and lead from the community of primary colonizers to the climax community.

serotinous Occurring late, as in plants that flower late in the year or events that take place late in the day.

solar constant The total amount of solar radiation in free space at the mean distance of the Earth from the Sun. It is approximately 1.36 W m⁻².

solarization The inhibition of photosynthesis that occurs at very high light intensity.

somatic mutation A mutation that affects a cell in the body (i.e. not a gamete) and that is transmitted only to those cells derived by mitosis from the cell carrying the mutation.

species diversity The number of species present in a particular area or community.

symbiont An organism that lives in symbiotic association with another.

symbiosis A situation in which two organisms of different species live together and are closely associated. The term generally implies some benefit to both, but is sometimes used to include parasitism.

synzoochory The collection of plant seeds by an animal and the storing of them for future consumption.

tectonic (*adj.*) Applied to a rock structure formed directly by movements within the crust (e.g. by faulting or folding).

tectonics The scientific study of the major structural features of the Earth's crust.

till Material that has been transported by a glacier.

trophic Pertaining to nourishment.

varve A layer of silt and sand deposited on the bed of a lake. Coarse, pale material is deposited in summer, dark, fine-grained material in winter, so each varve comprises one pale and one dark band. The sediment can be dated by counting the varves. Varves commonly form near the edges of glaciers.

weathering The breaking down of rocks into smaller particles by physical and chemical processes.

'white smoker' See black smoke.

xerophyte A plant adapted to arid conditions.

xerosere A sere (ecological succession) that begins in arid conditions.

zooplankton Plankton consisting of animals.



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