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J. L. Chapman and M. J. Reiss
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ONE

Introduction

1.1 What is ecology?

Ecology is the study of **organisms** in relation to the surroundings in which they live. These surroundings are called the **environment** of the organism. This environment is made up of many different components, including other living organisms and their effects, and purely physical features such as the climate and soil type.

Ecologists, those who study ecology, are always aiming to understand how an organism fits into its environment. The environment is of supreme importance to an organism and its ability to exist in the environment where it lives will determine its success or failure as an individual. This means that much of this book is really about the study of environments from the point of view of various organisms (but see Chapter 9 which describes in detail what makes up and affects an environment).

There are several definitions of ecology. Many workers have produced their own description of this branch of biology. The word ecology was first used by a German called Ernst Haeckel in 1869. It comes from two Greek words *oikos* meaning home and *logos* meaning understanding. Haeckel described ecology as 'the domestic side of organic life' and 'the knowledge of the sum of the relations of organisms to the surrounding outer world, to organic and inorganic conditions of existence'. This 'surrounding outer world' is another way of saying the environment. In 1927 Charles Elton wrote that ecology is 'the study of animals and plants in relation to their habits and habitats'. Today an ecologist would probably substitute the word 'organisms' for 'animals and plants' because we now recognise other categories of organisms (fungi, protoctists and bacteria) which are not in the plant or animal kingdoms. Many of these are extremely important in ecology although they are seldom as well studied as the plants and animals. More recently Krebs (1985) has defined ecology as 'the scientific study of the interactions that determine the distribution and abundance of organisms'. You may take your pick as to which definition you prefer.

Ecology is like an enormous jigsaw puzzle. Each organism has requirements for life which interlock with those of the many other individuals in the area. Some of these individuals belong to the same species, but most are very different organisms with very different ways of living or interacting. Figure 1.1 is a diagrammatic representation of this interlocking jigsaw. It illustrates some of the ways in which a single individual fits in with others. In this case an animal is represented which catches other animals for food (it is a predator) and which in turn is hunted and may be killed by another species of predator. During the animal's lifetime it needs to find a mate of the same species to produce offspring. During its life it also competes with other animals (**competitors**) for food and will probably catch diseases.

The ability of the animal to avoid the predator, catch its prey, withstand disease and so on will

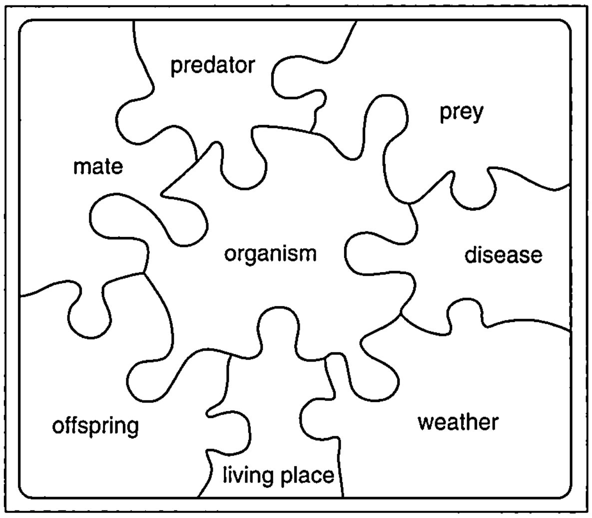

Figure 1.1 Diagram showing the interlocking nature of the features of the environment which influence an organism. In this case the organism is a predator, but to generalise the diagram, the word 'prey' could be replaced by 'food', or, for a plant, by 'light and nutrients'. For simplicity, this figure is two dimensional, but the ecological interactions of organisms and their environment are really multi-dimensional.

depend on the relationships it has with the organisms around it. Its life will also be affected by the weather, time of year and the quality of nesting or sleeping sites. In fact, this simplified example is already becoming complicated as more and more pieces of the puzzle are added. The study of these ecological relationships from the point of view of a single species, as is illustrated by Figure 1.1, is called **autecology** (see Chapter 3). If all the species living together are studied as a **community** (see Chapter 14) then this study is called **synecology**.

1.2 The nature of ecology

The only way to find out how any organism survives, reproduces and interacts with other organisms is to study it. This makes ecology a practical science. There are three main approaches to the study of ecology. The simplest method is to observe and record the organism in its natural environment. This is sometimes described as observation 'in the field' or **fieldwork**, although the term can be confusing as 'field' suggests open grasslands or the site of human cultivation. A second type of study is to carry out experiments in the field to find out how the organism reacts to certain changes in its surroundings. A third approach involves bringing organisms into a controlled environment in a laboratory, cage or greenhouse. This method is very useful as it is often easier to record information under controlled conditions. However, it must be remembered that the organisms may react differently because they have been removed from their natural home.

No single study can hope to discover everything there is to know about the relationships between an organism and its environment. These relationships are so varied that different kinds of investigation are needed to study them. Often both study in the natural environment and experiments in the laboratory are required to discover even part of the picture. Also, as the environment changes, so an organism may respond differently, with the result that an experiment under one set of conditions may well give different results to the same experiment carried out under different conditions.

So we have a picture of ecology as a subject full of complexity where an organism has many different responses and needs. Theoretically, therefore, there is an almost infinite amount to be discovered about the ecology of the world. Even after a century of ecological study we are just scratching the surface of possible knowledge. A large amount has been discovered over the years, but our knowledge is patchy; we know far more about northern hemisphere temperate woodland than we know about tropical rainforest, more about English rocky sea shores than the Australian barrier reef.

What makes ecology exciting, rather than an endless list of things to be learned about organisms, is that we are studying a living, working system. Because the system fits together so neatly it forms repeated patterns which can be recognised by the ecologist. Organisms with similar life styles often respond to their environment in similar ways. For example our predator in Figure 1.1 can only catch its prey in certain ways. If its prey becomes scarce it may starve, eat something else or migrate to where food is more plentiful. In other words it only has a certain number of options and its response to certain conditions may well be predictable. Understanding why organisms react to various conditions in one way rather than another takes us a long way towards an understanding of the principles of ecology.

These principles, with which this book is concerned, are only becoming understood because of the many studies of organisms both in the field and in the laboratory. Throughout this book you will find examples of how particular organisms relate to their environment given as evidence to support the principles being described. Because the relationship of organisms to their environment may be very subtle, it can often be difficult to unravel the situation to discover the principles involved. Yet finding out how organisms interact and applying these principles can be an absorbing and fascinating pursuit.

1.3 The study of ecology

An ecologist could start any study by asking the question: 'Why does this organism live or grow here and not there?'. In simplified terms this is the question ecological investigations often try to answer. Of course it is far too difficult to answer in one go and can be split up into many different questions. The first and most obvious question is: 'Where does the organism or species I am studying live?'. Usually this can be answered by careful observation in the field with the help of some sort of sampling method. Once we know this other questions may become obvious. For example an ecologist may ask:

How does the organism obtain its food?
Is a particular nutrient limiting its growth or numbers?
Is something else limiting its growth or numbers?
Does it reproduce in this site and if so how?
Is it absent from parts of the site due to some factor?
How and when do the young disperse?
What causes the death of the organisms?

There are numerous possible questions, some of which may be unique to a particular situation. Obviously, if an ecological investigation starts with specific questions, or objectives, it makes the task of studying the ecology of organisms much easier.

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Box 1
Experimental design

As so much of our ecological knowledge comes from experiments it is worth thinking about how experiments are designed. The skill and care with which an experiment is planned and carried out will affect the accuracy of the information collected and the way in which the results are interpreted. Be critical when reading other people's experimental techniques and their interpretation of the results. They may have made mistakes. Even if they have not, you will be practising the important scientific skill of looking at and analysing information with an open mind. Watch out for poorly designed experiments – there are several about, even in the literature! If you want to use some findings, but only have a report of the work by a third party, try to get a copy of the original publication. A tentative suggestion by a careful worker is easily turned into an apparent certainty by someone else.

There are several things to consider when looking at reported experiments or when designing your own.

(1) Is there a 'control'?

A **control** is an experiment which is specially designed to show the effects of the actual experimental technique (other than the factor being investigated) on the organisms under consideration. A control group of organisms is treated in the same way as the experimental group, except for the factors being studied in the experiment. For example, in an experiment which involves digging up plants and planting them in another site to see how well they grow under different conditions, a control would involve digging up plants and replanting them in the original place. From this control, the effects of digging up the plant (root damage, soil disturbance, etc.) can be determined and this can be taken into account when looking at the plants which have been moved to the new site.

(2) Are there replicates in the experiment?

The confidence with which conclusions can be drawn from an experiment is increased by repeating it several times (having **replicate** experiments) and considering all the results together. The more times the experiment is repeated and the results averaged the more likely the results are to be reliable. Statistical analysis of the results is then possible. Obviously hundreds of repeats would be time consuming, possibly expensive and no doubt tedious! So many would not improve the results enough to be worthwhile. Some experiments are impossible to repeat because some unusual situation is being recorded or because the species being studied is rare.

(3) Are the right data being collected?

Sometimes the wrong data are collected from an experiment or wrong recordings made during observation of organisms in their natural surroundings. It may be very difficult to decide in advance what information is valuable to the study, so the best advice is to collect as much as possible and select what to analyse later. For example, it is no good applying a nutrient to the soil in which plants are growing, and then analysing only the leaves of the plant to see how the nutrient has been used. The plant may be concentrating the nutrient in its roots! 'Out of sight – out of mind' is a phrase we often use in everyday situations, but it can also apply to ecological investigations. Many experiments would be improved by taking into account 'invisible' factors such as root activity, the effects of microorganisms and so on. Unfortunately these factors are often very difficult to study.

(4) Are the data correctly interpreted?

Because data from ecological experiments are often quite variable and sometimes inconclusive, it is often quite difficult to interpret the results. Occasionally classic mistakes are made, as was the case for the worker who moved a plant into a different locality. When he went back to see how it was growing in its new environment he 'found' that it had turned into a different species! What had actually happened was that his original transplant had died and another plant, native to the area, had grown in the space left there. Of course bad experimental design was involved, the plant was not adequately labelled and so the wrong conclusions were reached. This is an obvious mistake and we might think the worker silly and that we would never make such an error. However, the interpretation of experimental results is seldom as simple as we might expect.

Summary

(1) Ecology is the study of how organisms live and how they interact with their environment.
(2) The environment includes other organisms and physical features.
(3) Autecology is the study of the ecology of a single species.
(4) Synecology is the study of the ecology of whole communities of organisms.
(5) Ecology is a practical science requiring observations and experiments to investigate organisms.
(6) There are underlying principles in ecology which predict how organisms will react in particular circumstances.
(7) Experimental design is extremely important and requires, wherever possible, controls, replicates, the accurate collection of data and careful interpretation of results.

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TWO

The individual

2.1 Why look at individuals in ecology?

Although ecologists are often interested in the complex interactions between species, it is worth remembering that it is individual organisms that are the products of natural selection (Chapter 8). This chapter deals with the biology of individuals. Individuals are the fundamental units of populations, communities, ecosystems and biomes which are discussed in later chapters. In this chapter we will look at individuals from an ecological perspective. We will start with the essentials of how they obtain their energy and nutrients, and then consider how these are allocated to maintenance, growth and reproduction.

2.2 Autotrophs and heterotrophs

All organisms need energy to live and different organisms obtain this energy in different ways. There are many approaches to classifying the ways in which individuals obtain their food. A useful one is to divide organisms into **autotrophs** and **heterotrophs**. Autotrophs obtain only the simplest inorganic substances from their environment. Green plants are the most obvious autotrophs. These need only visible light, water, carbon dioxide and inorganic ions such as nitrate (NO_3^-) to survive, grow and reproduce. The process of **photosynthesis** enables most plants, the photosynthetic bacteria and some protoctists to synthesise all the complex organic molecules that they require from these simple building blocks. Because these organisms use light as their energy source, they are called **photoautotrophs**. **Chemoautotrophs** are autotrophs that obtain their energy not from sunlight but from certain specific chemical reactions involving only inorganic substrates. The ecological importance of chemoautotrophs and photoautotrophs is discussed in Chapter 11.

Animals, fungi, most bacteria, many protoctists and a few plants cannot synthesise their organic molecules from inorganic ones. They need to take in an external source of organic carbon. These organisms are heterotrophs.

2.2.1 *Terms associated with heterotrophic nutrition*

While autotrophs such as green plants and chemosynthetic bacteria obtain the few nutrients that they require from the environment around them, heterotrophs have first to **ingest** their food, if necessary **egesting** some of it too, and then to **digest** what they have ingested. Digestion is followed by **absorption**, and absorption by **assimilation**. Finally, some matter is **excreted**.

Ingestion

Ingestion is the process by which heterotrophs take in their food. The number of techniques used by heterotrophs to ingest their food is huge and is discussed in more detail in Section 2.2.2. For most animal species it is useful to distinguish two stages to ingestion. In the first, the food is captured; in the second, it is brought within the alimentary canal.

Egestion

In some animals not all the food that is ingested is eventually digested. For example, some time after an egg-eating snake has swallowed an egg it regurgitates the crushed shell. The eggshell is said to have been egested. Owls also egest pellets containing the fur, feathers and bones of the small animals they have eaten. In general, the parts of the food ingested by a heterotroph which have not been digested sufficiently to allow them to be absorbed into the tissues are disposed of by egestion. The faeces produced by animals also contain egested material. For example, the plant fibre in our diet, though important for the proper functioning of our large intestine, is not digested, but egested via the anus.

Digestion

Digestion is the process by which heterotrophs break down the food they have ingested into particles small enough to be absorbed. In most cases, this means

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that mastication and hydrolytic enzymes are used to break down food particles to their constituent monomers. Proteins are broken down to amino acids; carbohydrates to monosaccharides; fats to tiny fat globules or even to fatty acids, glycerol and other simple molecules. Salts and vitamins can be absorbed without needing to be digested.

Absorption

Absorption is the uptake from the gut of vitamins, salts and the products of digestion. In mammals these substances are absorbed by certain of the villi of the small intestine. The products of absorption are either respired or assimilated.

Assimilation

Assimilation occurs when the products of absorption are taken up by cells and synthesised into macromolecules. These macromolecules may be stored or used for repair, growth and reproduction.

Excretion

Excretion is a characteristic of all organisms, not just heterotrophs, and occurs when the waste products of metabolism are expelled from an organism. Nitrogen is an important excretory product of heterotrophic organisms. When proteins are broken down, ammonia (NH_3) is produced. Ammonia is very toxic and needs to be diluted in a large volume of water. Freshwater fish, which obviously have water in abundance, are able to dilute and then excrete their ammonia directly. Other vertebrates convert the ammonia to compounds which can be concentrated so as to be less wasteful of water, such as trimethylamine oxide, urea ($CO(NH_2)_2$) or uric acid.

The excretory products of one organism are almost invariably utilised by other organisms (see Chapter 13). For instance, the nitrogenous waste products of heterotrophs are typically converted to nitrates by soil bacteria and taken up by plant roots. Oxygen is an excretory product of plants yet is vital for all aerobic organisms.

2.2.2 *Ingestion by heterotrophs*

The way an animal feeds profoundly influences many aspects of its ecology. Heterotrophs differ greatly in the sorts of food they ingest and in the ways they obtain their food. Three main types of heterotrophic nutrition are commonly recognised.

Holozoic nutrition

Holozoons feed on relatively large pieces of dead organic material. Most of the animals with which we are familiar can therefore be described as holozoic. **Carnivores**, such as the fox (*Vulpes vulpes*), feed on prey which they have caught (Figure 2.1). **Herbivores**, such as sheep, cattle and goats, feed on vegetation. Animals which feed on a mixture of plant and animal food, such as the pig and most humans, are called **omnivores**.

Figure 2.1 A five month old fox cub (*Vulpes vulpes*) feeding on a hen pheasant.

Each of these terms may be subdivided. For example, herbivores include **granivores** (animals such as the world's most abundant bird, the redbilled quelea (*Quelea quelea*) which feed on grain or seeds), **frugivores** (which feed on fruit), **folivores** (which feed on the leaves of shrubs or trees), **grazers** (which feed on herbs and grasses) and **browsers** (which feed on the leaves, young shoots and fruit of shrubs and trees). Animals have anatomical, physiological and behavioural adaptations which are associated with their diets. Consider an animal such as a deer or antelope which grazes grass. Grasses contain very fine particles of silica (SiO_2), the same hard substance of which sand is composed. This silica wears away teeth, and many grazers, if predation is infrequent, die of starvation when their teeth literally wear away. Over the course of evolution grazers which can maintain the grinding surfaces of their teeth have been favoured by natural selection. The teeth of many grazers grow from their roots throughout their life. Elephants have responded to the problem of tooth abrasion in a remarkable manner. At any one point in their life they only have four grinding teeth in use, one in the upper and one in the lower jaw on each side. Each tooth, as it is worn down, is slowly replaced by another from behind. Should an elephant get to be more than about 60 years old, it will have used up all of its 24 teeth in this way.

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Figure 2.2 One to two day old swifts (*Apus apus*) infected by lice.

Figure 2.3 Many-zoned polypore (*Coriolus versicolor*) on a dead tree trunk.

Parasitic nutrition

Parasites, unlike holozoons, feed off matter that is still alive. Because of this, parasites are usually much smaller than their **hosts** (Figure 2.2). This means that they generally have shorter lifespans than their hosts and are more numerous than them. As well as being smaller than their hosts, parasites harm their hosts. The host gains nothing from the relationship and is therefore constantly selected to avoid being parasitised.

Parasitism is an evolutionary trait which has evolved independently in a huge number of different taxa. Indeed, parasites may be found in all five kingdoms – bacteria, protoctists, fungi, plants and animals. Parasites can conveniently be divided into **endoparasites**, such as tapeworms, which live inside their hosts, and **ectoparasites**, such as fleas, which live outside them. Whether endoparasitic or ectoparasitic, most parasites obtain their food in liquid form. Parasites of plants may obtain their nourishment from the phloem, as aphids do. Animal parasites may live in the gut or tap into the lymph or blood system.

Saprotrophic nutrition

Saprotrophs feed on dead organic matter which they either absorb in solution or ingest as very small pieces. Many fungi, for instance, are saprotrophs, living off dead organisms (Figure 2.3). Most saprotrophs obtain their food by extracellular digestion – enzymes are secreted on to the food source and the soluble products are then absorbed. This is the technique used by bacteria, fungi and the house fly (*Musca domestica*) for instance. On the other hand, earthworms obtain their food in solid form including small bits of dead leaves and soil invertebrates. Animals which feed off dead organic matter, but ingest large pieces, may be classified as **scavengers**. Spotted hyaenas, for example, often scavenge, though they obtain a large amount of their energy by hunting and killing prey.

2.3 Metabolic rate

One of the most useful single pieces of information an ecologist can have about an individual is its **metabolic rate**. The metabolic rate of an organism is the amount of energy it needs per unit time. This indicates what the demands of that organism are on its environment. For instance, animals with large metabolic rates are generally found near the top of food webs and at quite low population densities. A convenient unit for measuring metabolic rate is the number of joules of energy an organism uses each day. For organisms that rely on aerobic respiration to supply their energy needs, oxygen consumption is directly proportional to energy requirements and metabolic rate may be measured in units of hourly oxygen consumption as this is fairly easy to measure.

Organisms require energy in order to replace their tissues and make new ones for growth and reproduction. Organisms which burn up a lot of energy for their size, such as birds, are said to have a high metabolic rate. Organisms such as snakes, which can survive on much less food, are said to have a low metabolic rate. Many measures of metabolic rate have been made, of which perhaps the best known is **basal metabolic rate**. The basal metabolic rate of an organism is the minimum amount of energy it needs to respire to maintain life when the body is at rest and just ‘ticking over’. Three conditions need to be fulfilled for the metabolic rate of an organism to be its basal metabolic rate. First, the organism needs to be in a thermoneutral environment (so that no energy has to be used for thermoregulation). Second, the organism must be at rest (so that no energy is needed for locomotion or any other activities). Third, the organism has to be in a post-absorptive state (that is some time after food has been eaten) because the metabolic rate of an organism rises shortly after it eats.

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Box 2

Difficulties in the classification of heterotrophic nutrition

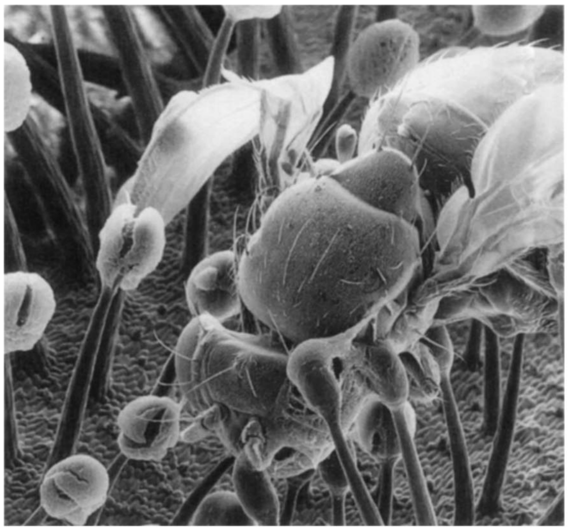

Figure 2.4 Scanning electron micrograph of the leaf of a Cape sundew (*Drosera capensis*) showing a fly which it has caught on its sticky hairs.

This chapter is full of definitions of words which ecologists use to describe organisms and the processes which go on inside them. Humans like to have their world defined and classified into boxes. Such classification, and the naming that accompanies it, helps us to communicate with precision. We classify all living organisms into species which have Latin binomials that are traditionally printed in italics (e.g. *Homo sapiens* is the binomial we give ourselves) or underlined in non-printed text. The science of classifying organisms is called **taxonomy**. It could be said that taxonomists are members of the oldest profession, because in The Bible it was Adam who named all the animals (*Genesis* 2)!

Ecologists also try to categorise or classify many aspects of the environment and the species they are studying. Many such classifications are attempts to order the organisms using some of the principles of ecology which have been discovered. For instance, species can be aggregated into communities and these can be grouped into the major biomes of the world (Chapter 17). Such ecological categorisations can lead to problems because, although there are underlying principles which can be found in ecology, there are also many exceptions to general rules. These exceptions are sometimes very valuable in giving us further insights to the principles themselves, but they do cause problems to the precise mind. Ecology is a science of averages and possibilities, not an exact discipline like some branches of physics or chemistry.

Some examples of the problems that arise when organisms are forced into a system of precise definitions can be seen in this chapter. Organisms can be described as autotrophic or heterotrophic and heterotrophs can be divided into holozoons, saprotrophs and parasites. This suggests that all heterotrophs fall neatly into one of these three exclusive categories. The truth is more complex. For instance, some parasitic organisms, once their host is dead, feed saprotrophically on its body. Some holozoic feeders also take in soluble food at times during their lives.

The whole classification gets even more difficult when some plants are considered. Although most plants are true autotrophs, some are completely parasitic, lacking any chlorophyll. The broomrapes (*Orobanche* spp.) are such a group. Each broomrape exists as an underground system of roots. These are attached to the roots of photosynthetic plants from which the broomrape obtains sugars and other substances. Only the brown or purple flowering spike appears above ground to be pollinated by insects.

There are other species of plants which have such parasitic root connections, but also contain functioning chloroplasts. Such species are **hemiparasites**. This means that they obtain only some of their nutrients parasitically, the rest being made autotrophically. Eyebrights (*Euphrasia* spp.) fall into this intermediate category. It is quite probable that many more plant species are hemiparasitic than we realise. Digging out complete root systems is a painstaking and unenviable job! However, once it is done, it quite often turns out that apparently normal autotrophic plants have root connections with other plants. Radioactive tracers have been used to see whether such root connections enable the movement of photosynthates from one individual to another.

Finally, what about plants like the sundew (*Drosera capensis*) shown in Figure 2.4? Sundews have modified leaves which bear sticky hairs. Should an unfortunate insect come into contact with these hairs it may be unable to break free. The leaf then curls up, holding the insect tight and enabling the plant to digest it. The sundews are often described as being carnivorous as are other plants which rely on animal matter, such as pitcher plants (*Nepenthes* spp.) which trap insects in their flask-like leaves, and the Venus fly-trap (*Dionaea muscipula*) which actively catches prey by snapping shut a modified leaf when an insect lands on it. In each of these cases the insect is digested outside the plant: extracellular enzymes are secreted by the plant and the soluble products are then absorbed. In some cases the insect is dead before digestion begins. Such nutrition is better described as saprotrophic rather than carnivorous. On the other hand, in those cases when the insect is alive at the start of digestion, the nutrition could be described as ectoparasitic – the parasitic plant attacking the live prey from the outside! It is probably best not to spend much time puzzling about how to classify heterotrophic nutrition. It is more fruitful to spend the time investigating it.

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To an ecologist, measurements of *basal* metabolic rates are not especially useful. For one thing, the concept of a thermoneutral environment only applies to homoiotherms (endotherms). Anyway. ecologists are more interested in what an organism's energy expenditure is in real life. Nagy (1987) provides a useful catalogue of the various terms that have been used to refer to realistic estimates or measurements of the **daily energy expenditure** of organisms in the field. Daily energy expenditure includes the energy spent on locomotion, thermoregulation, growth and reproduction. It is usually about 1.5 to 3.0 times basal metabolic rate (Gessaman, 1973; King, 1974; Lucas *et al.*, 1993). In humans and other vertebrates, the maximal sustained energy consumption over 24 hours is about 7 times basal metabolic rate (Hammond & Diamond, 1997). In principle, both basal metabolic rate and daily energy expenditure can be measured for any organism. In practice, almost all the measurements have been made on animals at least several millimetres in length. Ecologists have tended to concentrate on larger species, partly because of the difficulties of measuring the metabolic rates of very small organisms.

2.4 Factors affecting metabolic rate

2.4.1 *Size*

Perhaps the most important factor affecting the metabolic rate of an individual is its size. Figure 2.5 shows the basal metabolic rates and daily energy expenditures for 47 species of birds plotted against their body mass (Bennett & Harvey, 1987). Overall, larger birds need more energy each day to live. However, metabolic rates are not directly proportional to body mass. If they were. then the points on the graph would fall on a steeper line indicated by the thin dotted line. In fact the slope of the actual relationship is shallower than this. A bird ten times heavier than another one does not need ten times as much food each day. The relationship between metabolic rate and body mass can be expressed by what is called the **allometric equation**:

$$\text{Metabolic rate} = a(\text{body mass})^b$$

In this equation, b is referred to as the **exponent** that relates metabolic rate to body mass. If logarithms of both sides of this equation are taken, it can be rewritten as:

$$\log[\text{metabolic rate}] = \log[a] + b(\log[\text{body mass}])$$

A log–log equation like this is plotted in Figure 2.5. From such a graph, a and b can be worked out, as a equals the metabolic rate when body mass is 1 and b is the slope of the line. Measurements on a number of different taxa show that the exponent, b, relating metabolic rate to body mass lies between about 0.5 and 0.9, irrespective of the units used for the measurements either of metabolic rate or of body mass (Kleiber, 1947; Peters, 1983; Reiss,. 1985). Values for b tend to lie close to 0.75. The reasons for this are only now becoming understood. They are complicated but, at least in multicellular organisms, may be to do with the need to transport essential materials within individuals by means of space-filling fractal networks of branching tubes (West *et al.*, 1997). (Fractals are explained on page 181.) Because b is less than 1.0, larger species need *less* energy per day, *relative to their body mass*, than do smaller species. This means that small animals, such as shrews, have such a high metabolic rate relative to their body size that they may need to eat more than their body weight in food each day! An elephant, on the other hand, takes about three months to eat its own body weight of food.

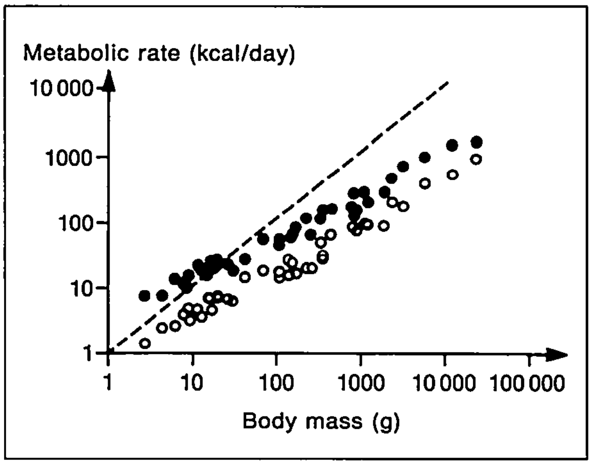

Figure 2.5 Daily energy expenditure (●) and basal metabolic rate (○) in kcal/day (one kcal is 4198J) on logarithmically scaled axes for 47 species of birds for which both values are available. Dotted line shows what the slope of the relationship would be if metabolic rate was directly proportional to body mass. (From Bennett & Harvey, 1987.)

2.4.2 *Life style*

Even among organisms of the same size, there is a great deal of variation in their metabolic rates. In a classic analysis Hemmingsen (1960) compared the basal metabolic rates of unicellular organisms, **poikilothermic animals** and **homoiothermic animals** (Figure 2.6). As you might expect, homoiotherms, which maintain a constantly high body temperature, need a lot more energy than poikilotherms. It is perhaps surprising just how much energy they need. As Figure 2.6 shows, a homoiotherm needs about 25–30 times as much energy as a poikilotherm of the same size. It is a lot cheaper to feed a pet snake weighing 5 kg than a pet dog weighing 5 kg!

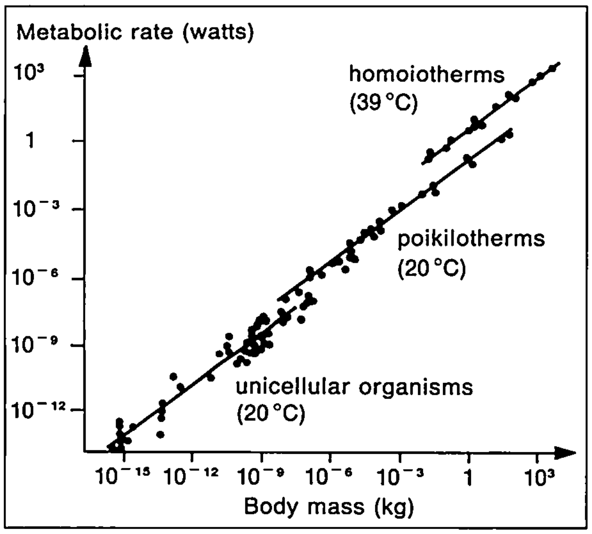

Figure 2.6 Basal metabolic rates of homoiotherms, poikilotherms and unicellular organisms as functions of their size. (From Peters, 1983.)

It is interesting to note, from Figure 2.6, that a poikilotherm has a metabolic rate some 8–10 times higher than a unicellular organism of the same size. Evidently there is quite an energetic cost to being multicellular.

If you look at Figure 2.6, you can see that much of the variation within the three groups – unicellular organisms, poikilotherms and homoiotherms – can be accounted for by body size. However, there is considerable scatter about the three lines. Attempts to identify the reasons for this scatter have mainly focused on birds and mammals. Essentially, two reasons for the variation can be suggested: life style and phylogeny. For example, mammals that feed on vertebrates have high basal metabolic rates relative to other mammals (Elgar & Harvey, 1987a). It might therefore be that a mammal that eats vertebrates needs a high basal metabolic rate because of its life style, perhaps because it must constantly be ready to rush after its prey. As Elgar and Harvey point out, however, the association might have a quite different explanation. It turns out that the correlation among mammals of high basal metabolic rate with the eating of vertebrates is mainly due to the possession of both of these traits by whales and dolphins (Cetacea) and seals (Pinnipedia). Perhaps the high basal metabolic rates of these animals reflect their marine life styles rather than their feeding habits. Of course, this too would be an ecological explanation for their relatively high basal metabolic rates. Alternatively, perhaps all cetaceans and pinnipeds have high basal metabolic rates irrespective of their ecology. This would mean that their high basal metabolic rates might be due to phylogeny rather than to life style. Another possible explanation arises from the fact that it is extremely difficult to measure the basal metabolic rates of seals and dolphins under laboratory conditions. They stress easily and often show abnormally high 'basal' metabolic rates. It might therefore be that the high values are an artefact.

2.5 Size determines more than metabolic rate

As we have seen, size is a very important determinant of an organism's metabolic rate. However, there are many other features of an organism's life that are strongly affected by size. Table 2.1 gives the values of the exponents relating various physiological. anatomical, ecological and behavioural measures to body mass. For instance, a value of 0.17 for incubation time in birds means that the length of time birds of different species spend sitting on their eggs is related to the mass of the parent bird by the equation:

$$\text{Incubation time} \propto (\text{body mass})^{0.17}$$

and this will be true irrespective of the units in which either incubation time or body mass are measured. Some exponents are negative. For example, the one relating heartbeat frequency in mammals to body mass is –0.25. This means that heartbeat frequency is related to the body mass of different mammals by the equation:

$$\text{Heartbeat frequency} \propto (\text{body mass})^{-0.25}$$

In other words. the larger a mammal is, the smaller the number of times its heart beats each minute. The smallest shrews have heartbeat frequencies of over 1200 times a minute.

We can conclude that an organism's size greatly influences its ecology. Knowing an individual's size immediately tells us something about how it interacts

Table 2.1 Exponents relating various anatomical, physiological, ecological and behavioural variables to body mass in the equation variable $\propto$ (body mass)^{b}. Taken from Peters (1983), Schmidt-Nielsen (1984) and Swihart *et al.* (1988).

Variable	Taxon	Exponent (*b*)
Home range size	Mammals	1.26
Skeletal mass	Rattlesnakes	1.17
Skeletal mass	Mammals	1.09
Skeletal mass	Fish	1.03
Lung volume	Mammals	1.02
Ingestion rate	Crustaceans	0.80
Brain mass	Mammals	0.70
Gestation length	Eutherian mammals	0.24
Age at maturity	Fish	0.20
Incubation time	Birds	0.17
Heartbeat frequency	Mammals	−0.25
Breathing rate	Mammals	−0.26

with other organisms and with the rest of its environment. In particular, the amount of energy an organism takes in each day is closely related to its body size. But what do organisms do with this energy? How much of it can they apportion to growth or to reproduction and how much do they need just to remain alive? These questions can be answered by looking at the energy budgets of organisms.

2.6 Energy budgets

Why do organisms take in food? We take eating so much for granted that this sounds like a silly question. However, it is worth emphasising that evolutionary success, for any organism, is judged by how successful it is at reproducing itself. It is an extraordinary thought that *every* individual alive today has an ancestry that goes back some 3500 million years, yet many of the individuals alive today will themselves fail to leave any offspring behind, the first in their line thus to fail. Organisms take in food so that energy and nutrients can be channelled towards the production of offspring.

Individuals cannot devote all their resources directly to reproduction. Some of their energy intake is needed to keep themselves alive and in good condition. In fact, around 10 to 30% of the energy absorbed from food ends up being used to digest food (Cossins & Roberts, 1996). When individuals are juvenile, they devote some of their energy to growth. Presumably, in most cases, a juvenile individual that tried to reproduce would not be very successful at it. For one thing, it would be too small to leave many offspring. It is more likely to maximise its **lifetime reproductive success** by waiting until it has grown more. Chapter 7 looks at the ecological pressures favouring growth or reproduction and at the conflict between reproduction and mortality: an individual that devotes too much of its resources to reproduction runs the risk of killing itself in the process. In this section we will look quantitatively at what happens to the energy that individuals ingest.

2.6.1 *Assimilation efficiency*

As we discussed at the beginning of this chapter, when an organism ingests food, only some of it is assimilated. The term **assimilation efficiency** refers to the percentage of the energy that an organism ingests that is assimilated rather than egested. As one might expect, organisms differ greatly in their assimilation efficiencies depending on the type of food they eat. Carnivores feeding on vertebrates may have assimilation efficiencies in excess of 90%; insectivores typically have assimilation efficiencies of 70–80%, while most herbivores have assimilation efficiencies of 30–60%, though zooplankton feeding on phytoplankton have assimilation efficiencies of 50–90% and the giant panda (*Ailuropoda melanoleuca*) has the lowest assimilation efficiency of any mammal yet measured at 20% (Ricklefs, 1980; Anon, 1982).

Assimilation efficiencies can be much lower than 20%. Cammen (1980) drew together data on the feeding habits of 19 species of invertebrate deposit feeders and detritivores found on the ocean bottom and which belonged to three phyla. The percentage of organic matter in the sediment on which these species fed ranged from 57% down to less than 1%. The crab *Scopimera globosa* fed on the poorest quality food, which contained only 0.19% organic matter. This means that the assimilation efficiency of *Scopimera globosa* must be less than 0.19%. Measurements on the contents of the foregut of this species show that there the food has on average an organic content of 12% (Ono, 1965). This means that a great deal of egestion must have taken place before the food reaches the foregut.

2.6.2 *Production and respiration*

Once a heterotroph has assimilated its food, the products of assimilation can either be respired to provide the energy needed to maintain existence and to repair old and damaged body tissue, or they can be diverted to growth and reproduction. Together, growth and reproduction are called **production**.

The percentage of the energy assimilated that an organism diverts to growth is called its **growth efficiency**. Growth efficiencies are economically very important to farmers. Juvenile pigs have growth efficiencies of up to 20%, which is very high for a farm animal. This means that pigs are very efficient at converting their feed into pig meat. The efficiency of this conversion is affected by many factors. As one might expect, their growth efficiency is highest when they do not have to expend any energy on thermoregulation and movement. Under intensive production some farmers therefore keep pigs warm and in almost total darkness – pigs move less when it is dark.

For any species, growth efficiencies are higher the smaller the individuals are, relative to their size at maturity. Figures 2.7a and 2.7b show growth efficiencies as functions of size for Leach's storm-petrel (*Oceanodroma leucorhoa*) and the fish *Ophiocephalus striatus*. In each case the growth efficiency decreases as the individuals mature. Because of this, it is rather difficult to make comparisons between species about their growth efficiencies. Nevertheless, as a general rule, juvenile poikilotherms have higher growth efficiencies than juvenile homoiotherms. However, if one looks at the growth efficiencies of *very* young organisms, one finds that homoiotherms may have growth efficiencies as high as 50–70%, almost the same as