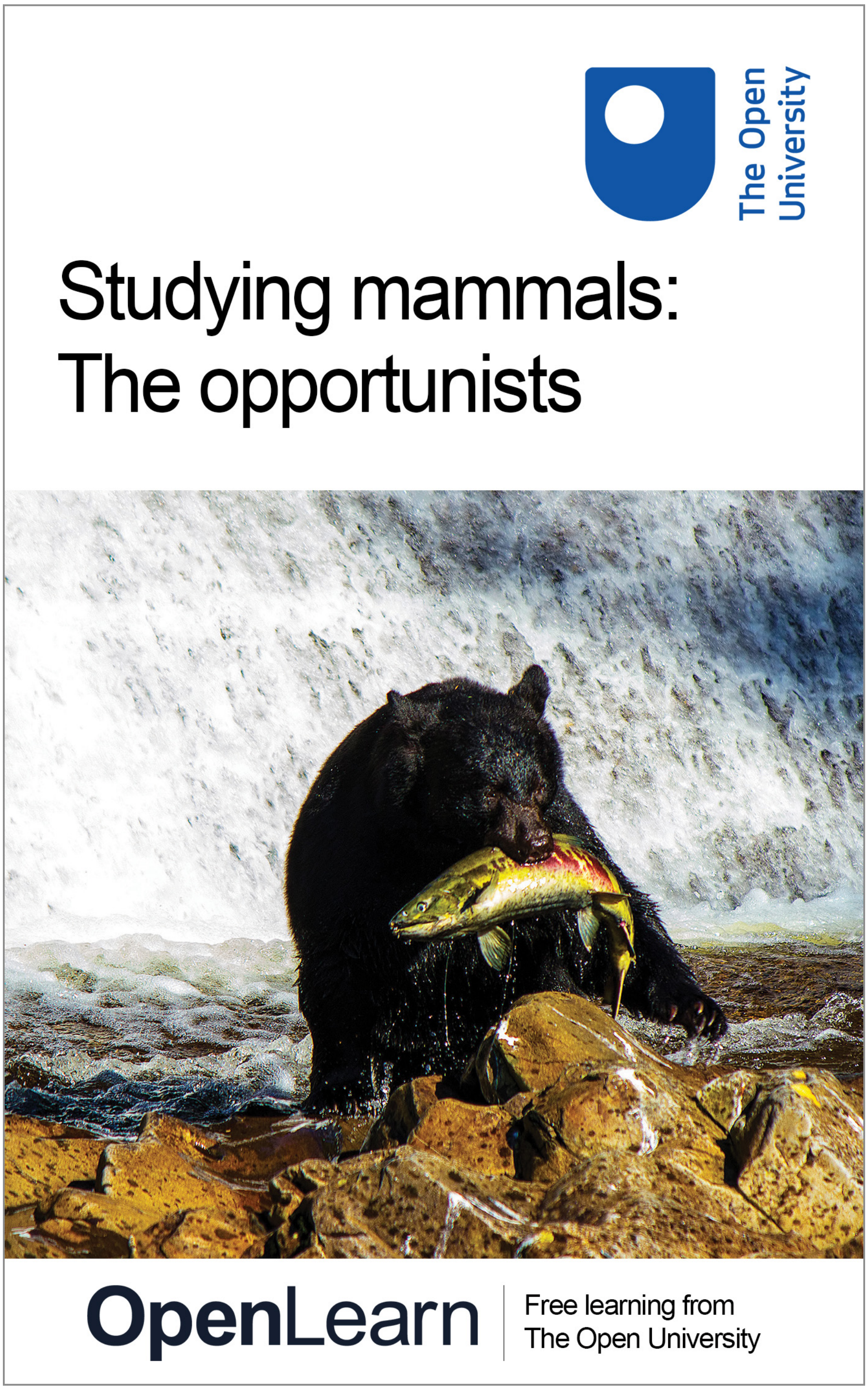
Studying mammals: The opportunists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Studying mammals:
The opportunists
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Introduction

That mammals need energy to support all aspects of their lives, be it breathing, running, excreting, repairing cells, reproducing, keeping warm, is a central, unifying theme of the 'Studying mammals' series of units. So is the notion of specialisation of diet - that mammals display adaptations, i.e. specialised teeth or complex stomachs, that enable them to cope with the demands of particular diets. This course addresses these two related themes of energy and of specialisation. Why might omnivorous mammals have 'broken the rules' and adopted a much more wide-ranging diet than the carnivores and herbivores? This course will tell you about their biology, mixing examples of mammalian diversity with the identification of characteristics that are common to many omnivores.

This is the sixth in a series of units about studying mammals. To get the most from these units, you will need access to a copy of *The Life of Mammals* (2002) by David Attenborough, BBC Books (ISBN 0563534230), and *The Life of Mammals* (2002) on DVD, which contains the associated series of ten BBC TV programmes. OpenLearn course S182_8 *Studying mammals: life in the trees* contains samples from the DVD set. You should begin each course by watching the relevant TV programme on the DVD and reading the corresponding chapter in *The Life of Mammals*. You will be asked to rewatch specific sequences from the programme as you work through the course.

This OpenLearn course provides a sample of level 1 study in Environment & Development

Learning Outcomes

After studying this course, you should be able to:

- explain the concept of energy transfer between trophic levels
- outline the usefulness and limitations of food chains and food webs
- using examples, weigh up the value of dietary specialisation and of omnivory
- summarise the physiological changes linked with ‘hibernation’ in grizzly bears
- give examples of variations in diet and lifestyle among the bear family.

1 The omnivores

As you work through this course you will come across boxes, like this one, which give you advice about the study skills that you will be developing as you progress through the course. To avoid breaking up the flow of the text, they will usually appear at the start or end of the sections.

As well as the course text, you will be using *The Life of Mammals* book (LoM) and related *The Life of Mammals* DVDs, as described in the introduction to this course. Before you go any further, watch 'The Opportunists' on the DVD and read LoM Chapter 6. Unless stated otherwise, all the page references you encounter in this course will be to LoM.

Diet plays a very important role in the life of mammals. They are often categorised, as is the case in LoM, according to what they eat, for example, herbivores and carnivores. Dividing up mammals in such a way offers insights into mammalian biology that wouldn't be so apparent had LoM followed a more orthodox taxonomic approach, focusing perhaps on different mammalian orders in turn. This approach reveals the diversity of mammals - their varying dentition and differences in their reproductive habits, for example - against a background of their common features, such as the need to fuel a relatively high body temperature via the intake of substantial amounts of energy-yielding food.

That mammals need energy to support all aspects of their lives, be it breathing, running, excreting, repairing cells, reproducing, keeping warm, is therefore a central, unifying theme of the 'Studying mammals' series of units. So is the notion of specialisation of diet - that mammals display adaptations, i.e. specialised teeth or complex stomachs, that enable them to cope with the demands of particular diets. This course returns to these two related themes of energy and of specialisation, building on the topics covered in prior units in the series, but in each case offering a fresh perspective. For the first theme (in Section 2), I'll be concerned with how the energy contained within foodstuffs passes between different organisms, between prey and predator for example, and what this process reveals about the interactions and interdependencies between organisms with different diets, mammals included. Such issues are central to the branch of biology known as ecology; ecological ideas are essential to understand what makes particular populations of interacting organisms 'tick'.

Learning more about how energy flows between different organisms raises the question of how mammals satisfy their energy demands by being *specialist* feeders. Having said so much in earlier units about the features associated with the diets of insects, plants or other animals, and dwelt on the presumed advantages of such lifestyles, why might omnivorous mammals of the type you have just read about in LoM have 'broken the rules' and adopted a much more wide-ranging diet? LoM Chapter 6 offers many examples of such opportunistic feeders and this course will tell you a good deal more about their biology, going beyond the level of detail that LoM provides. You'll know from LoM that omnivores have by definition a wide-ranging diet but, unlike carnivores for example, there is no defined taxonomic group called 'Omnivora'. Rather, the habit has developed in a whole range of mammalian groups. So in what follows you can expect an account that mixes examples of mammalian diversity with the identification of characteristics that are common to many omnivores.

2 The ecology of mammals

2.1 Trophic levels

'All flesh is grass'; this somewhat paradoxical biblical quotation really is only a restatement of what was more formally explained in previous units in this series. The materials needed by plant eaters (see course S182_4) for the growth of 'flesh' - by which I mean not just the meaty muscular parts, but all of the body - must come entirely from their plant food. Plants grow using the Sun's energy in the process of photosynthesis. Plants occupy the lowermost of a succession of feeding levels, a position known as trophic level 1 (trophic means related to nutrition). The herbivores that were the subject of S182_4 therefore occupy the next level up - trophic level 2. Those carnivorous animals feeding on herbivores, of the type discussed in course S182_5, must therefore be in trophic level 3. They have the capacity to use some of the energy and materials locked up in the 'plant-eater flesh' food that they consume to build up their own bodies. Thinking in terms of energy flow through these levels, a proportion of the solar energy captured by plants in trophic level 1 has passed through into trophic levels 2 and 3.

Question 1

Question: Relationships are often expressed as flow charts, where annotated boxes are linked by arrows. Sketch a flow chart to show the movement of solar energy through different trophic levels.

Answer

solar energy → plant material (trophic level 1) → plant-eater flesh (trophic level 2) → animal-eater flesh (trophic level 3)

What this simple relationship reveals is that animals depend on plants for their energy supply - a dependence evident in the use of the term 'primary producer' (or more simply 'producer') to describe plants in trophic level 1; herbivores and carnivores are termed primary and secondary consumers respectively. What is also evident is that in any feeding relationship, in addition to the materials in food passing from one organism to another - such as calcium from the soil into grass and hence into rabbits and then into stoats to help build bones - there is also a flow of energy. In the next section, you'll meet a number of examples of particular feeding relationships, identifying 'what eats what'; these are more formally termed food chains. As you'll see, a great many food chains have a plant at the bottom; at the top is an animal that is eaten by no other. The organisms that interact in this way exist within a particular ecosystem, which is the collective term used for all the living and non-living components that make up a particular part of the environment.

2.2 Energy flow in ecosystems

You are about to meet some very large numbers, expressed in scientific notation, and some new units. The new units are those that are used to measure the amount of solar energy received by a part of the Earth's surface. Since plants are dependent on light for photosynthesis, the amount of plant material that can grow in a particular area depends, to a large extent, on how much solar energy reaches it. Energy is measured in joules (J) or, more often, in thousands of joules (kilojoules, kJ). The number of kilojoules received depends on the size of the area and the duration of the period of measurement. If we take an area of one square metre (1 m^2) and measure the solar energy received during a whole year, then the units will be kJ per m^2 per year, or more scientifically, kJ m^{-2} $year^{-1}$. The 'year' is not strictly an SI unit and you may meet several different abbreviations, such as 'yr' (used in this text), 'y', or sometimes 'a', the abbreviation for 'annus' or, when preceded by 'per', 'annum'. Geological time is often quoted in Ma (millions of years).

An enormous amount of solar energy reaches the surface of plants, but most is reflected away and only a small proportion can be used by the plants for photosynthesis. The amount of solar energy falling on typical grassland is 7×10^6kJ m^{-2} yr^{-1} (i.e. 7000 000 kJ m^{-2} yr^{-1}).

Question 2

Question: Of this large amount of solar energy, only a relatively small amount ends up in plant material - about 85 000 kJ m^{-2} yr^{-1}. Express this value as a percentage of the total amount of incoming solar energy.

Answer

The units quoted here are identical (kJ m^{-2} yr^{-1}), so you need to divide one measure by the other and multiply by 100, i.e.

$$(85\,000 \text{ kJ m}^{-2} \text{ yr}^{-1} / 7\,000\,000 \text{ kJ m}^{-2} \text{ yr}^{-1}) \times 100\% = 1.2\%.$$

In other words, the efficiency of energy conversion of the primary producers is only 1.2%. (Note that I initially retained the units as I set up this calculation, which is good scientific practice, but since they were the same at the top and bottom of the fraction, they must be cancelled and the final value is simply a percentage.)

Let's think more about the origins and fate of the food produced by plants via photosynthesis. Plants are not so much 'making' or 'producing' energy as 'converting' the energy of sunlight into chemical energy in the form of sugars - a biochemical trick that no animal can perform. So for plants, sugars are the initial products of photosynthesis; animals have to obtain these complex raw materials from their diet, and after digestion break them down into the smaller, usable chemical fragments, some of which are then metabolised to yield energy. In plants, some of the sugars produced go towards building up new plant material - forming, for example, the 'building blocks' for cellulose.

Other sugars in plants are broken down to yield the energy needed to sustain life processes - just one example is the energy needed to synthesise complex carbohydrates, such as cellulose. Energy that is used up in the plant's own metabolism in this way isn't 'locked up' in the form of the plant's cells and tissues, so is therefore not available to herbivores that might eat the plants. This 'lost' energy can no longer flow to the next trophic level. Another fraction of energy is lost as some plant tissues die - leaves in autumn, for example - and are subsequently consumed by bacteria and fungi.

Such energy losses mean that only a fraction of the material produced by photosynthesis in plants is eaten by the animals in the next trophic level - the herbivores, which comprise primary consumers. The transfer of energy to trophic level 2 is therefore limited. In our example, of the 85 000 kJ m^2 yr^{-1} converted to plant material, only 39 000 kJ m^{-2} yr^{-1} may be consumed by the herbivores. But not all of this consumed food and energy can be 'captured' by herbivores and turned into herbivore flesh - the indigestible fraction ends up as faeces and a sizeable fraction is used to fuel the metabolism of the herbivores. In our case, about 6200 kJ m^{-2} yr^{-1} is captured by primary consumers, which leads to a calculation of trophic efficiency of herbivores (i.e. the fraction of energy locked up in their food that is converted into 'plant-eater flesh' of level 2 consumers) of (6200 kJ m^{-2} yr^{-1}/39 000 kJ m^{-2} yr^{-1}) × 100%=16%.

At each transfer between trophic levels, energy is lost. If only 16% of the food or energy taken in is converted into 'plant-eater flesh' then 84% of the energy is lost from the food chain. (Bear in mind that this energy isn't strictly speaking lost, in the sense of being destroyed - the law of conservation of energy, which you may have heard of, allows only its conversion to another form. What is meant here is simply that such energy is lost from the food chain - the lost energy pops up in another form and ultimately all of it is 'lost' as heat.) This loss of energy at each stage explains why there are tens of millions of plants in an ecosystem, but only thousands of herbivores and only tens of carnivores. In the vast areas of African grassland in Botswana, Kenya and Tanzania, huge grazing and browsing herds of herbivores can be maintained, but these support a much smaller number of meat-eating hunters. The proportion of energy flowing from one level to another is variable, but as a good rule of thumb we can think of 10% being transferred to the next trophic level, which helps explain why relatively few such levels are evident in ecosystems.

2.3 Food chains and food webs

This section includes two graphs. Figure 2 has the standard numerical values on its axes, in this case years from 1830 to 1930 on the horizontal axis and number of lynx furs traded, from zero to 60 000, on the vertical axis. Figure 1 does not have any numbers, although similarly the horizontal axis represents time and the vertical axis represents the number of animals; the arrow by the label shows the direction in which the values are increasing. A graph of this type is often referred to as a 'sketch graph', since it is the shape of the graph, in this instance the general changes in the numbers of animals as time passes, that matters. The precise numbers and the exact amount of time varies depending on the species of animal being studied. Sketch graphs are often used in science to show general trends or to illustrate the general situation.

A particular feeding sequence, of the type described in LoM in a real-life situation, comprises a food chain in which particular primary producers and primary and secondary consumers are identified.

Question 3

Question: Using information from LoM Chapter 5 and the TV programme 'Meat Eaters', draw food chains ending in (a) the stoat and (b) the African hunting dog (see course S182_5). Include the trophic levels and use the terms primary producer, primary consumer and secondary consumer.

Answer

trophic level:	1		2		3
	primary producer		primary consumer		secondary consumer
(a)	grass	→	rabbit	→	stoat [pp. 124-127]
(b)	grass	→	impala	→	African hunting dog [pp. 136-140]

Such food chains reveal the relationships between species. As I've mentioned, they not only reflect the movement of the constituents of food (the example I gave earlier was calcium) moving from one organism to another, but there is also flow of energy. You now know that loss of energy is inevitable between levels; for example, for an impala to gain 1 kg in weight it needs to consume 10 kg of bush vegetation and then only 10% of the impala's mass is assimilated by its predator, the African hunting dog.

These food chains suggest, for example, that a large population of rabbits will flourish only if there is good growth of grass in the area around the warren.

The population of rabbits will be cut back by the stoats, in the gruesome manner you saw in the programme 'Meat Eaters' at 102.12, but obviously if the stoats kill all of the rabbits, there will be no food for them. If the rabbit population in an area crashes because of disease, the reduced grazing allows the vegetation to grow taller but the local population of stoats may also crash.

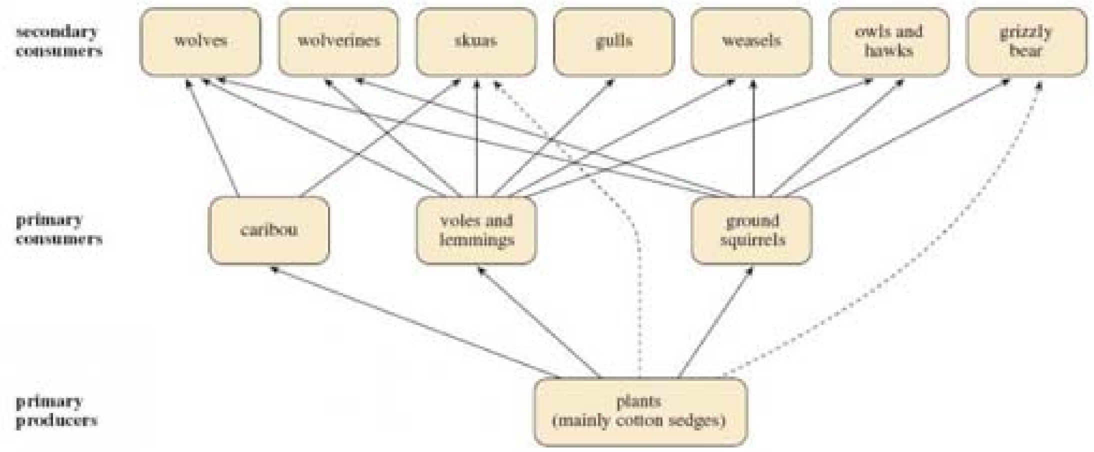

Figure 1 A sketch graph of changes in predator and prey numbers over time. For each axis, the units are arbitrary

Figure 1: adapted from Cadogan, A. and Best, G. (1992) *Environment and Ecology*, Thomas Nelson and Sons Ltd

Figure 1 : adapted from Cadogan, A. and Best, G. (1992) *Environment and Ecology*, Thomas Nelson and Sons Ltd

Figure 1 is a simplified view of changes in predator/prey numbers in any one area over a period of time. Early in the period of study, a decline in the number of predators (the red line), perhaps as a consequence of lack of hunting success, allows numbers of prey (blue line) to increase. But prey eventually become sufficiently numerous to support an increase in the population of predators. Their hunting success on such a grand scale may eventually lead to a fall in numbers of prey (the blue line falls after a peak) which, after a lag period, in turn leads to a fall in predator numbers, after which the cyclical pattern may be repeated.

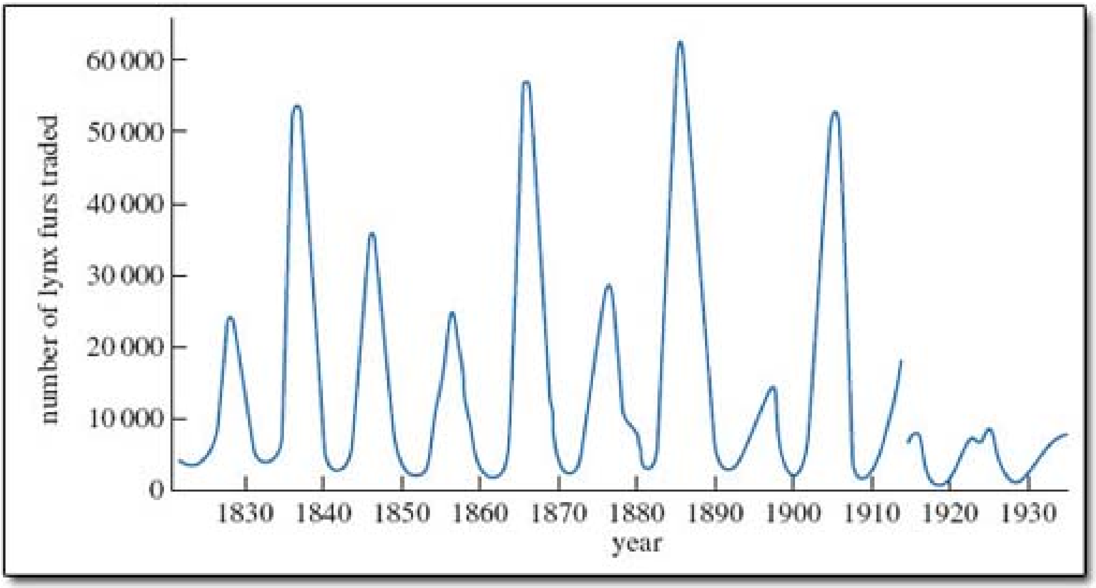

Figure 2 Number of lynx furs traded between the 1820s and 1930s by the Hudson's Bay Company. (There is a break in the record between 1910 and 1920.)

Figure 2: adapted from Cadogan, A. and Best, G. (1992) *Environment and Ecology*, Thomas Nelson and Sons Ltd

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A good example of a fluctuation of this type can be seen in records of the Canadian lynx population. Records of skins of trapped animals (numbers of skins, for fur, are related to population size) sold to the Hudson's Bay Company show that over a period of 100 years or so there were peaks in the lynx population every nine or ten years (see Figure 2). These changes appear to be related to the size of the population of the snowshoe hare, which is a very significant prey item for this carnivore. Number of snowshoe hares is in turn influenced by shortages of grass upon which they feed, perhaps after especially hard winters.

Of course, changes in ecosystems over time normally reflect shifts in a number of dependent factors. Most primary consumers, for example, eat more than one type of plant - the koala is a notable exception. Most carnivores prey on more than one species and, given the likely unreliability of supply of any one prey species suggested in Figure 1, the reason is obvious. Any over-specialised consumer - perhaps a population of stoats feeding exclusively on rabbits - would pay a high price for their narrowness of diet if prey numbers collapsed. So, a population of primary consumers is likely to be part of more than one food chain, such that different chains interconnect, forming a food web. These more varied and complicated relationships suggest that omnivorous feeding - the subject of much of the remainder of this course - is likely to be a widespread habit, evident once we start to draw up food webs.

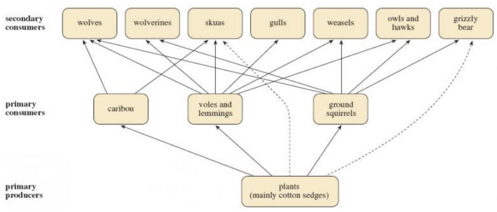

Figure 3 A food web for one particular location within the Arctic tundra, based upon

protracted ecological study in that area. This habitat is dry and very cold and is north of the forest line. Notice that some animals that are classed as secondary consumers may include plants in their diet (dashed lines)

Figure 3: adapted from *Biology for the IB Diploma* (2001) Oxford University Press

Figure 3: adapted from *Biology for the IB Diploma* (2001) Oxford University Press

Figure 3 shows a food web for one part of the Arctic tundra, with primary consumers that range from diminutive lemmings to very sizeable caribou.

Question 4

Question: LoM Chapter 5 and the programme 'Meat Eaters' describe the feeding habits of two mammals that inhabit the tundra - the grey wolf and the arctic fox. LoM Chapter 6, and especially the programme 'The Opportunists', very vividly illustrate feeding of grizzly bears. How fully are the feeding habits of these three mammals illustrated in Figure 3?

Answer

Surprisingly, the arctic fox doesn't feature in Figure 3, though it is a typical inhabitant of the tundra. It has a wide variety of prey, including lemmings and gulls [pp. 128-129], but also eats fruit, along with carrion of marine mammals, as David Attenborough (DA) mentions. If gulls are classed as secondary consumers, as in Figure 3, the arctic fox could be classified as a tertiary consumer, though an extra tier on the diagram might start to over-complicate it. (Incidentally, wolverines, medium-sized carnivores that are members of the weasel family [p. 178], are known to prey on caribou, often as carrion - another link not apparent in Figure 3.) LoM p. 131 describes wolves as preying on North American bison, which are animals of the prairies rather than tundra; those represented in Figure 3 feed on the less-fearsome caribou. But these wolves are also obliged to prey upon smaller mammals when caribou migrate to their summer feeding grounds. In 'The Opportunists' you saw the highly omnivorous grizzly bear feeding on roots, grass, the carcass of a whale, deer, salmon, clams and berries - a much more wide-ranging diet than implied by Figure 3.

What this example illustrates is that no single, simple food web can do justice to the complexities of an ecosystem. Even with a modest number of species 'boxes', a complete representation of feeding habits can swiftly lead to a confusing multitude of criss-crossing lines! Given that many mammals - and especially omnivores - have very wide-ranging diets, food webs in such cases will be far from the clear representations that they purport to be. Feeding habits change with time too - salmon are only periodically available to grizzlies, as very often are caribou to wolves. Feeding relationships displayed for one location of an ecosystem may not hold true for another. Neither do food webs reflect the energy transferred as organisms die and enter another food chain of breakdown and decomposition. The energy transfer at these stages is into scavengers - fly larvae and burying beetles are familiar examples - and into bacteria and fungi. For such reasons, some ecologists are distinctly lukewarm about the benefits of trying to encapsulate complexity in 'simple to read' food webs. Nevertheless, the drawing up of food webs and the tracing of energy flows underpins a good deal of modern ecological research, combining precise measurements with the approximations and simplifications that are inevitably part of any branch of biological science.

You've encountered different types of diagram in Section 2. Inevitably they are simplifications of the real thing - and they leave out details and assumed irrelevancies. Sometimes diagrams try to capture the essential features of three-dimensional 'reality' or perhaps a vertical section of a leaf or the structure of a human eye, as in previous units in this series. Flow charts of the type you drew for yourself earlier express an idea, in the form of a relationship between different components. They encapsulate the key information that might otherwise take many hundreds of words to describe - why not attempt to use one to summarise an idea or a section of text at this point? Other diagrams convey some form of relationship between two different quantitative variables. All such diagrams inevitably simplify and sometimes distort, or represent things out of context. The familiar adage of 'those who simplify, simply lie' adds a useful note of caution, but getting the most out of diagrams and drawing up your own - useful for consolidating your own learning - is an important part of study.

3 Is specialisation always advantageous?

Specialisation generally implies the possession of adaptations that make animals particularly effective or efficient in one or more aspects of their lives. In many of the examples used in other units in this series, mammals are likely to possess adaptations related to the acquisition and/or processing of food.

Question 5

Question: What is the most accessible and frequently used indicator of a mammal's diet in both living and fossil species?

Answer

A mammal's dentition often gives a very good indication of the sort of food to which it is adapted.

Insect eaters (course S182_2) usually have relatively small, sharp teeth (for example, tenrecs [p. 51]) or lack them altogether (as do anteaters). Some grazers have blade-like incisors with which they cut clumps of vegetation (course S182_4) and most have large molars which they use to grind the food before swallowing it. Many of the carnivores in course S182_5 have a veritable armoury of stabbing canines, slicing carnassials and bone-crushing molars.

Question 6

Question: What is the main advantage to a group of mammals of developing adaptations - in particular, dentition - that enable it to specialise in the food it eats?

Answer

Possession of appropriate adaptations, enabling a group of mammals to specialise in a particular sort of food, probably makes it more efficient at exploiting that food resource than any of its potential competitors.

However, there is inevitably a 'down side' to specialisation. If, for any reason, a food resource becomes less available than formerly, a highly specialised mammal would probably be unable to compete effectively for alternative food resources, because other mammals would already be more efficient at exploiting these resources.

You'll be aware that several groups of mammals have adopted an entirely different strategy when it comes to food. In effect, they have specialised in being non-specialists. These mammals have acquired and retained the ability to turn to a wide range of different food resources according to availability. It is to the biology of these opportunistic feeders - the omnivores - that we turn our attention in the remainder of this course.

4 The bear necessities

4.1 The grizzly bear

There are three activities in Section 4, asking you to summarise information in the form of lists. In the first two, the answers are given but in the third, about the diet of the giant panda, they are not. You are asked to tick off the points in your list as you read on through the section. As you gain more study experience, you should feel less dependent on the answers always being provided in full. Aim to take more responsibility for your own learning and to judge for yourself whether you have answered the questions appropriately. When you have completed Section 4, check whether you spotted all the points that I have included. You may even be pleasantly surprised to find that you've included some that I've missed!

As DA points out [p. 159], most members of the bear family are omnivorous. The grizzly bear is a particularly magnificent member of that family.

Activity 1

Watch the sequence from 23.02-30.49 in 'The Opportunists' and make a list of the different sorts of food that the grizzly bear utilises during the course of a year.

Answer

You should have compiled an impressive list: fresh-caught salmon, berries, sedges, grasses, caterpillars and clams. Grizzlies probably eat *many* other sorts of food not covered in the programme. Indeed, LoM also mentions horsetails, skunk cabbage, lily roots, elderberries, cranberries, mice, squirrels and marmots [p. 159].

Not only do grizzly bears eat a great diversity of foods, in certain seasons they also eat prodigious quantities. During late summer - as they lay down reserves of fat that enable them to survive the impending winter - they may eat for 20 hours a day. One female grizzly in Alaska was observed eating nothing but blueberries for 14 hours, with only 30 minutes off for a midday rest; the TV programme gave a figure of 200 000 berries per day. The digestive system that bears have inherited from their carnivorous ancestors lacks the special stomach that enables herbivores to break down plant material so efficiently. Their inability to extract much of the energy it contains helps explain why bears harvest vast amounts of plant material, a proportion of which passes through their guts unaltered. Indeed, grizzlies are believed to play a very significant ecological role, simply through the distribution of undigested seeds in their dung.

DA mentions [p. 159] the 'delicacy' that the grizzly bears of Yellowstone Park enjoy in summer. The fact that the highly digestible bodies of tiny cutworm moths comprise 18% protein and 35% fat in mid-August makes it less surprising that grizzly bears are prepared to climb to 10 000 feet (3000 m) in Yellowstone and elsewhere to feed on them. It is possible that the bears see birds, such as ravens, Clark's nutcrackers and grey-crowned rosy finches, flying up to the high country and know that it is time for them to go there as well. But how did they discover that the birds were going there to feed on the thousands of moths hiding under rocks during the day so that they were in position to feed on alpine flowers at night?

The TV programme (27.57-30.18) emphasises the importance of laying down 'energy reserves' during summer feeding, mainly as fat - you'll recall the process of (in the words of the commentary of the programme) 'piling on the calories' during the summer bonanza. The mobilisation of these reserves is what sustains the grizzly over the 5- to 6-month period of overwintering in its den, during this unique type of hibernation.

Question 7

Question: In what respects is this type of hibernation in the grizzly bear different from the examples of hibernation given in course S182_2, for example in the European hedgehog?

Answer

In the hedgehog, body temperature drops as low as 5 °C (S182_2 Figure 8); DA talks of a body temperature drop of only 'several degrees' in the grizzly (authorities quote a drop from 38 °C to 34 °C). But the heart rate of the grizzly falls substantially 'to about 10 beats per minute' according to the commentary, which is not a great deal different from that of the hedgehog. Hedgehogs arouse spontaneously from hibernation, though the purpose of these periods of being warm remains largely unknown; other small hibernators use these periods to drink, eat stored food and eliminate waste. Most authorities take the view that an overwintering grizzly does none of these things, even during the occasional moments of 'stirring' from its prolonged sleep referred to in the TV commentary at 24.07.

Indeed, overwintering in bears is such a very different physiological phenomenon from the true hibernation discussed in S182_2, that many biologists prefer the term winter dormancy (or winter lethargy) to describe it. Since the term hibernation is used in LoM (and the TV programme) we shall use it here, but as DA points out [p. 159] winter sleep in bears is different from 'true' hibernation, and indeed, an ability to survive this degree of suspension of bodily functions for up to six months is unique amongst mammals. It involves a high metabolic price too - maintaining a body temperature (T_b) of 34 °C for this period helps explain why the demands on the bear's energy reserves are so severe. You'll recall calories being counted down in the programme, with the burning up of 'a million calories' according to the commentary. All the more intriguing to puzzle, therefore, why this expensive physiological trick evolved in bears.

Question 8

Question: Can you think of any advantages of a form of hibernation where a high T_b is maintained? Thinking about the size of the bears as well as their reproductive habits might help.

Answer

Bears remain responsive and alert to danger if T_b is maintained. Perhaps the risks of discovery during this type of hibernation - by wolves or possibly other bears yet to establish a den - are very great. The size of bears is likely to be a factor too - mammals this big are not able to hide! A substantial drop in T_b during hibernation will necessitate a substantial energetic investment when hibernation ends - and perhaps during periodic spontaneous arousal. This is manageable for small mammals, where the amount of heat required to warm the body mass is relatively modest; but for animals as large as a grizzly, reheating on this scale may be physiologically impossible. Finally, for the female, it may that a high T_b is necessary to support the development of the cubs that, as DA mentions, are born as the mother 'dozes' [p. 162]. Bear cubs are very small at birth relative to adult size, and need to grow quickly if they are to withstand the rigours of the following winter. Lactation requires a high level of metabolism.

Whatever the reason, or combination of reasons, there is much to learn from the grizzly about this type of hibernation. But you'll appreciate that it takes a particularly intrepid biologist to enter the den of a responsive, overwintering grizzly, armed only with a determination to further scientific knowledge. Little wonder that so much more is known about hibernation in the hedgehog than in the grizzly.

4.2 Other members of the bear family

Other omnivorous species of bear include the Asian black bear, the North American black bear and the Andean spectacled bear. Although polar bears spend their winters hunting seals out on the Arctic sea-ice, they have to come ashore when the ice melts in spring and find other sources of food.

Activity 2

Reread LoM p. 165 and make a list of what the polar bear lives on when it is unable to hunt seals.

Answer

Your list should be quite similar to that for the grizzly bear: small mammals, such as ground squirrels and lemmings (though such prey are taken by polar bears very infrequently); vegetation, such as roots and sedges; and fruit, such as blueberries, cranberries and crowberries. Male polar bears will also eat the young of their own species, on the rare occasion they get the chance. (Infanticide is a surprisingly widespread habit amongst mammals. There is more about this in S182_9 *Studying mammals: the social climbers*.)

The polar bear is strongly specialised to hunting seals and is the only largely land-based animal that does so. You'll know from LoM that there are a few other bears that appear to have travelled down the road of dietary specialisation. While the Malayan sun-bear [p. 165] eats the eggs and nestlings of ground-nesting jungle fowl and the larvae of termites whenever an opportunity arises, it feeds predominantly on fruit - although it also has a penchant for the honey of wild bees. The front claws and snout of the sloth bear are adapted to breaking into termite hills and then sucking up termites - you probably recall the sequence in the TV programme (31.30-32.46) demonstrating (with suitable sound effects) the 'hoovering up' of termites. The lips are large and floppy and two front upper incisors are absent. However, even this degree of specialisation presumably makes the sloth bear less efficient at hunting small mammals or eating vegetation, though it is competent enough at feeding on honey, when it withstands the stings of honeybees to raid honeycombs.

The member of the bear family that has moved furthest from being an omnivore towards having a highly specialised diet is the giant panda.

Activity 3

Watch the TV programme from 00.31-02.18 and also reread LoM p. 156. List the adaptations displayed by the giant panda that allow it to live on a monotonous diet of relatively indigestible bamboo shoots. What are the advantages and disadvantages of this diet for the giant panda?

Answer

Tick off points on your list as you read the following section of text.

The giant panda's molar and carnassial teeth are adapted for crushing and grinding tough, silica-impregnated bamboo shoots. The animal has a large muscular stomach in which it can retain this material for 10 hours to process it further. However, the giant panda's most bizarre adaptation is that which American palaeontologist Stephen Jay Gould wrote about so eloquently in *The Panda's Thumb*, one of his collections of essays devoted to evolutionary topics:

> I was delighted when the first fruits of our thaw with China went beyond ping pong to the shipment of two pandas to the Washington zoo. I went and watched in appropriate awe. They yawned, stretched, and ambled a bit, but they spent nearly all their time feeding on their beloved bamboo. They sat upright and manipulated the stalks with their forepaws, shedding the leaves and consuming only the shoots.
>
> I was amazed by their dexterity and wondered how the scion of a stock adapted for running could use its hands so adroitly. They held the stalks of bamboo in their paws and stripped off the leaves by passing the stalks between an apparently flexible thumb and the remaining fingers. This puzzled me. I had learned that a dextrous, opposable thumb stood among the hallmarks of human success. We had maintained, even exaggerated, this important flexibility of our primate forebears, while most mammals had sacrificed it in specialising their digits …
>
> So I counted the panda's other digits and received an even greater surprise: there were five not four. Was the 'thumb' a separately evolved sixth finger?
>
> (S. J. Gould (1983) The Panda's Thumb: More Reflections in Natural History, pp. 20-21, Penguin Books)

Anatomically, the giant panda's 'thumb' is not a finger at all. During the course of evolution, it was constructed by gradual enlargement of a wrist bone (the radial sesamoid, Figure 4) together with some muscles. It provides an excellent example of pre-existing features becoming adapted, under the influence of natural selection, to serve an entirely different purpose; this is an example of preadaptation.

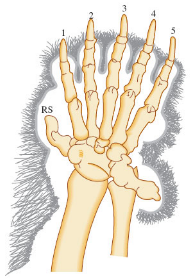

Figure 4 The giant panda's 'thumb' consists of an enlarged wrist bone (the radial sesamoid, RS). It is additional to the normal mammalian complement of five fingers, labelled 1-5. As Gould describes, the action of the 'thumb' helps giant pandas handle their food with considerable dexterity, in that it can be moved towards one or other of the clawed digits. The musculature associated with the RS (not shown here) is considerable, and ensures a degree of manoeuvrability that is not possible for the protruding bony structure on the opposite side of the paw

Bamboo is not very nutritious, though the shoots - which the pandas prefer - contain more nutrients and are more digestible than the mature stems. Giant pandas in the wild have to eat for up to 14 hours a day, consuming 12-38 kg of bamboo (i.e. up to 40% of their body mass).

The very indigestibility of the bulk of the bamboo plant means that only an extreme specialist can utilise bamboo as a food resource - although such a degree of specialisation must make it very difficult (if not impossible) for the animal to make use of any other sort of food. So, the advantage of specialising on bamboo is that the giant panda effectively has almost exclusive use of a food resource that was probably much more abundant in former times.

As you'll recall from LoM [pp. 156-158], the disadvantage is that periodically (between 15 and 120 years, depending on the species) *all* the plants of any particular species of bamboo flower just once and then die. When this happens, the giant panda has no option but to turn to another species of bamboo until the first has grown again from seed. Before humans reduced the bamboo forests to remnants, the giant panda probably had little difficulty doing this. Today, it cannot migrate in search of a different species of bamboo and consequently it has become a highly endangered species.

As DA writes 'Specialism is a high-wire act - spectacular when it is successful but catastrophic if there is one small failure' [p. 158]. One has to ask, therefore, why one species in an apparently successful family of omnivores turned so emphatically to such an extreme form of dietary specialisation and adaptation that it is now on the verge of extinction. The answer must be that, initially, there was an immediate selective advantage in becoming a specialist bamboo-eater. Only with the benefit of hindsight can it be seen that the giant panda now finds itself in what could be described as an evolutionary cul-de-sac from which it is extremely unlikely to be rescued by the operation of natural selection.

Question 9

Question: There's perhaps a danger of thinking of omnivory as being the ideal 'jack-of-all-trades' feeding tactic, permitting animals to switch from one food source to another as the occasion demands. What disadvantages might omnivory present?

Answer

To complete the familiar epithet, the disadvantage is that omnivores will be 'masters of none'. Being specialised with regard to a particular food generally means that something close to the maximum energetic gain is assured. Of course, the net gain from a meat diet is greater than from an equivalent mass of plant material, but the specialised plant-eaters in course S182_4 generally have adaptations that ensure maximum benefit from their more frugal diet. Mammals that feed opportunistically on plants tend to have a lower trophic efficiency (recall Section 2.1). An example would be the grizzly bears you read about in Section 4.1, which have to compensate by eating substantial amounts of plant material.

As you were reading this section, were there any questions that sprang to mind? For example, did you read the figures about how much bamboo a giant panda eats each day and wonder how much a panda weighs, or ask yourself what percentage of your body mass you eat in food each day? Perhaps you undertook a calculation as follows:

> 40% of the body mass of the giant panda is 38 kg.
> Let's represent the unknown body mass as BM.
> 40/100 (i.e. 40%) of the BM we know is equal to 38 kg.
> Therefore 1/100 (i.e. 1%) of the BM is equal to 38/40 kg.
> 38/40 kg is equal to 0.95 kg.
> Therefore 100% of BM is 0.95 kg × 100, which equals 95 kg.

You could undertake a similar calculation to work out how much food you would have to eat to consume 40% of your body mass per day.

On the other hand, perhaps you wondered about the dentition of giant pandas, or how its thumb evolved, or whether the sloth bears are the same species as the unfortunate 'dancing bears' that are paraded in front of tourists in India, or any of a host of other things. Responding in such a way is an encouraging sign of engagement with the text - you're not simply passively absorbing what you read. Getting involved with the text you read takes practice and requires a good measure of confidence. And finding out for yourself some answers to such questions makes studying more fun, and helps you explore particular aspects that interest you.

5 Miss Piggy

As the earliest mammals - the insectivores - were specialists, it follows that the omnivore lifestyle must have arisen at some later stage in a group or groups of non-omnivores. In fact, both seed eating and leaf eating arose before omnivory. Twenty million years ago, *Dinohyus* was undoubtedly a 'specialist' omnivore.

Activity 4

Reread LoM pp. 167-168 and note down the features that have convinced palaeontologists that *Dinohyus* was an omnivore.

Answer

As usual, the animal's teeth provide the most significant clues. As DA writes 'it had a set of generalised all-purpose teeth that could tackle most foods'. Its incisors did not especially equip it for the grazer's habit of nipping off grass and neither did it have the sort of canines that would be expected in a carnivore. Moreover, *Dinohyus* had a long snout and disproportionately large olfactory lobes in its brain, features which suggest that it had an acute sense of smell. It seems likely, therefore, that *Dinohyus* was a genuine omnivore and an early member of the pig family.

So the clinching evidence that *Dinohyus* was an omnivore comes from its dentition plus the indications that the animal had some kind of face decorations - modestly reflected in the computer reconstruction in the TV programme (05.37). Its presumed good sense of smell is also a tell-tale sign, and is all the more compelling evidence if you review the importance of this sense in relation to eating habits in present-day members of the pig family.

Activity 5

Watch the TV programme from 04.44-12.47 and reread LoM pp. 168-170, making notes relevant to the following topic. Describe in up to 200 words the various sorts of food consumed by different living members of the pig family and the extent to which a good sense of smell plays a role in locating any of these foods.

Answer

The babirusa uses its sense of smell to locate fruits of the Pangi trees (TV programme, 08.12). (The male's tusks are certainly the most bizarre upper canines you will encounter in the 'Studying mammals' units. However, they are not linked with feeding - they comprise a sexual display, important in the male-to-male fights that you saw briefly in the TV programme.) The European wild boar eats acorns, beech mast, chestnuts, ferns, earthworms, snails, frogs, lizards, mice and carrion. It also uses its sense of smell to locate truffles, an ancestral habit made use of by humans when they train domestic pigs for this purpose. Peccaries eat cacti. The bush pig ploughs up the ground in its search for roots, corms and bulbs. The giant forest hog eats mainly grass. The red river hog eats mainly fallen fruits. The warthog eats roots and tubers, the leaf bases of grasses and tree bark. The precise ways in which these animals use smell to locate food is unknown, but in the 'wild pig and boar' family as a whole, this sense may well be as important as vision - perhaps more so; the eyes of such animals are generally small.

On this basis, there can be no doubt that members of the pig family are omnivores *extraordinaire*.

6 The good family Procyonidae

As DA comments, this family is such an odd and varied collection that it doesn't have a common name [p. 170]. Its most familiar member (after which the family is named) is the raccoon, but the 19 species that comprise the family include mammals as diverse in habits and feeding preferences as the raccoon dog, the kinkajou and the red panda.

There is considerable taxonomic controversy about the members of the raccoon family - including the status of the red panda. With the kinkajou, early taxonomists saw a superficial resemblance to lemurs, so it was incorrectly classified as a primate. The fact that this animal is mentioned in a number of units reflects the inevitable shortcomings of any scheme that tries to divide up mammals into discrete types. Modern taxonomists classify the kinkajou (along with all other members of the raccoon family) as a carnivore and on those grounds it warrants a mention in S182_5 *Studying mammals: meat eaters*. But following the logic of the LoM chapters, its feeding habits locate it within the chapter on omnivores, alongside the olingo [p. 174], which is also a carnivore in taxonomic terms, though partial to fruit. On the basis of the kinkajou's feeding preferences, it is more accurately termed a frugivore, i.e. a fruit eater; its diet is 90% fruit and 10% leaves and nectar. Such complications remind us that ominvory must have developed independently many times in the course of mammalian evolution, which explains its patchy occurrence across the taxonomic groups. Where opportunities have arisen for the exploitation of food sources, mammals have shown a striking capacity to respond.

Activity 6

Reread LoM pp. 171-177 and describe the various foods eaten by different members of the family Procyonidae.

Answer

Raccoons apparently eat ripe raspberries, as well as worms, crayfish, small fish and frogs - all of which are hunted by making use of acute hearing and a very delicate sense of touch. (The tastes of the urbanised raccoons that you saw in the TV programme (35.55) must be even more varied.) The coati - and coatimundi - eat fruit, spiders, millipedes, lizards, nestling birds and mice, making great use of a long, narrow, mobile nose. The cacomistle and the olingo eat fruit, insects, birds and small mammals.

These procyonids can most definitely be described as omnivores. However, as I've indicated, it seems that the kinkajou is evolving towards dietary specialisation. The red panda - just like the seemingly unrelated giant panda - is committed to a specialist diet of bamboo. The fact that it also has the beginnings of a pseudo-thumb, enabling it to strip the leaves from bamboo stems efficiently, is a wonderful example of convergent evolution - whereby two species *independently* arrive at effectively the same solution to a common problem.

Question 10

Question: What other examples of convergent evolution have you encountered in other 'Studying mammals' units?

Answer

In the golden mole and the marsupial mole (S182_2), similar adaptations in unrelated animals have evolved, linked in each case with movement through sand. There are other examples in S182_7 *Studying mammals: return to the water*.

7 Of rats and men

The two most successful species of omnivore - humans and the brown (or Norwegian) rat - both arose within mammalian groups that are not particularly omnivorous. Most members of our own family, the primates, are exclusively or predominantly herbivorous. However, chimpanzees do occasionally hunt and eat monkeys and the human species is far from being exclusively vegetarian. Brown rats are rodents and almost all rodents use their continuously growing incisors to feed on seeds, nuts, grass, stems, roots, etc. Nevertheless, DA provides an amazing list of items apparently acceptable as food by brown rats: all parts of any plant, slugs, fish, insects, meat, bone, hair, hide, guts, toenails, beeswax, soap, cardboard, lead pipes, concrete and the plastic covering of electric cables [p. 179]!

Can it be coincidental that these two species (rats and humans) - so successful in terms of both population size and geographical range - have avoided becoming encumbered with restrictive adaptations to particular diets in their evolutionary past? Are there omnivore characteristics that have been brought together in these two mammals that may have contributed more generally to their current levels of success as species?

8 What makes a successful omnivore?

From what has been said already, there's good evidence that the key physical characteristic of the great majority of omnivores is a non-specialist dentition. What about other aspects of their biology?

Question 11

Question: Many omnivores (e.g. bears, pigs) have a good sense of smell. To what extent do you think that this might be another defining characteristic of omnivores?

Answer

Many carnivores (e.g. brown hyenas) also have an excellent sense of smell and, indeed, so do most herbivorous prey species (e.g. deer, antelopes). Perhaps a good sense of smell is a defining characteristic of mammals in general, rather than omnivores in particular. Even then, since humans don't have a particularly well-developed sense of smell, this does not appear to be a universal feature of mammals.

Apart from their non-specialist dentition, there may be no *physical* characteristics that are common to all or most omnivores among the mammals. How about *behavioural* characteristics?

Activity 7

From your viewing of the TV programme and your reading of LoM Chapter 6, list examples of behaviour related to feeding that might be regarded as typical or characteristic of omnivores.

Answer

Examples that you might have suggested are discussed in the text that follows. Tick off items on your list as you meet them.

One striking behavioural characteristic of all omnivores is their opportunism. Omnivores must be prepared to switch rapidly from one food resource that may be running out at the end of its 'season' to another as it becomes available. Thus, grizzly bears switch easily from salmon, to berries, to moths. Furthermore, many omnivores must be *taught* what is suitable as food and - presumably - what is not (for instance, because it is poisonous). This surely implies quite a good memory and what must be regarded as at least a rudimentary form of 'intelligence'. How do the babirusas featured in the TV programme at 09.30 'know' that a certain sort of clay can neutralise the poisons in their favourite Pangi tree fruits? Much the same question could be asked of comparable behaviour in tapirs, which are herbivorous browsers. The sequence at 12.07-18.35 in the TV programme 'Plant predators' of elephants excavating for minerals in the caves of Mount Elgon makes the same point, this time in the context of mineral deficiency; the photograph in LoM p. 114 implies that early learning plays an important part in maintaining this tradition.

Perhaps related to opportunism is inquisitiveness. Raccoons (and brown rats) apparently investigate *any* potential new source of food, as you might have surmised from the account of their feeding habits in the TV programme. In this they are greatly aided by their well developed senses of smell and touch, particularly since both operate in the dark to a large extent. Although there are great opportunities to exploit previously untapped food resources, there are also very obvious dangers. Brown rats are extremely cautious about nibbling unfamiliar food and consequently it is remarkably difficult to poison them. They also have the ability to associate particular tastes and smells with unpleasant experiences for at least 12 hours, which helps them to avoid repeating earlier mistakes. On the other hand, brown rats obviously do learn about new situations extremely quickly.

Over the years, scientists who study animal behaviour have conducted many interesting experiments to try to understand such learning. Working with white laboratory rats in the 1940s and 1950s, American psychologist Edward Tolman proposed that rats are able to construct what he termed cognitive maps of their environments. While a cognitive map should not be thought of in literal terms like a street map of London, experimental evidence certainly seems to suggest that the relative locations of relevant objects in the 'real' world are somehow stored in the rats' brains.

In one of his experiments, Tolman used the maze shown in Figure 5. Three paths (A, B and C) lead from the start to the goal box (which contains food). When given a free choice of paths, rats preferred to take path A, this being the shortest and most direct route. After a preference had emerged for path A, a block was placed at location X. Rats then preferred path B, the second shortest route. When the block was moved to location Y, the rats switched without hesitation to path C. Tolman argued that their cognitive maps of the apparatus enabled them to 'see' immediately that Y, which blocked path A, would also block path B but not block path C.

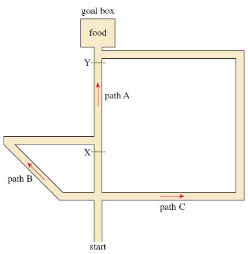

Figure 5 Maze employed by Tolman to demonstrate the possibility that rats develop cognitive maps of their environment

Since those pioneering experiments, a great deal of experimental work appears to confirm that rats possess something akin to cognitive maps of their environments. Of course, it's a far cry from the simple and artificial world of the laboratory to the more subtle and complex world of a mammal's environment, and no doubt these mapping abilities are called upon to a very great degree, in ways that remain unknown to us. But such maps are not unique to, or even exceptionally well developed in, omnivores. More than likely, the hunting carnivores, for example, have the same capacity.

Despite their renowned ability to switch rapidly from one type of food to another, even omnivores can be faced with periods when *none* of their usual food resources is available to them - for instance, during the depths of high-latitude winters. Under such circumstances, two general coping strategies are available to them.

Both require the deposition of food resources - either externally (perhaps caches in the ground) or internally (as fat) - that can be used to see them through these times of shortage.

The red fox - an omnivorous member of an otherwise carnivorous family - lays down food caches during times of plenty to help it survive harder times. You saw evidence of this in the TV programme (17.00-18.38), in the wake of the fox's raid on chickens. Although this habit - like many other aspects of its behaviour - implies that this species has a sophisticated memory, let's not rush to conclusions. It's possible that foxes simply regularly visit and systematically search 'preferred areas' and/or locate their food caches by smell rather than from memory. There's much the same uncertainty surrounding the use of acorn stores in squirrels.

The second option that omnivores use for overwintering is hibernation. The diversity of hibernation strategies is a useful reminder of just how variable the biology of omnivores has proved to be. You will have encountered the raccoon dog in the TV programme (13.00). It resembles both a raccoon and a dog, but taxonomically it is closer to the latter; it belongs to the family Canidae and the order Carnivora. It eats a huge range of foods, e.g. reptiles, small mammals and fruit. These it eats in great quantities in the autumn, when it can increase its body mass by up to 50% before entering true hibernation, i.e. it lowers its body temperature (T_b) to a few degrees above freezing. The raccoon dog is the only member of the dog family that can hibernate, but it does so comparatively rarely and only in parts of its range and when food is scarce. By contrast, raccoons have, as you've seen, a wide taste in food; they become inactive over the winter months, but are not true hibernators. I've already described a form of hibernation in the grizzly bear; what is not observed in grizzlies (for reasons I explored) is the very substantial drop in T_b typical of true hibernators.

It is appropriate to end, as DA does in LoM Chapter 6, with comments about the reputed success of omnivores. S182_1 *Studying mammals: winning design* presents a range of possible criteria by which to judge success: number of species, fossil presence in the geological record, geographical distribution. S182_3 *Studying mammals: chisellers* talks of the high productivity of rodents. Certainly, the family to which brown rats belong (Muridae) is successful by more than one measure. It consists of about 1300 species. As DA points out, the brown (or Norwegian) rat is one of the most widely distributed mammals in the world. To some degree, this enormous range reflects the effectiveness of the opportunistic, omnivorous habit. Further evidence comes from studies of contemporary human societies living in traditional, often hunter-gatherer style. These show just how varied and readily adaptable the human diet can be. The likely ability of our ancestors to vary and improve the quality of their diet and increase the efficiency with which they obtained food and extracted nutrients was probably a major 'driver' for the evolution and success of our own species. With only a small risk of exaggeration, we could say that omnivory made us what we are.

Conclusion

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