Studying mammals: Plant predators

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Contents

Introduction

The plant predators, or herbivores, are a varied group, but they share certain characteristics. Many of them are large; among the smallest is the chevrotain (or mouse-deer) at about two kilograms weight, and the elephant is the largest, with a typical bull male weighing around six tonnes. In this course we'll be looking in more detail at some of the problems and consequences of adopting a plant-eating way of life. Leaves are a much less nutritious food than most kinds of animal material, so large herbivores have to eat large quantities of plants and they have special ways to digest their food. We will look at how leaves work and the ways in which herbivores are adapted to survive on their plant-based diets.

To get the most out of this course 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. 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:

- describe the particular problems in digesting plant material
- give examples of the ways in which teeth are modified for a herbivorous diet
- explain the importance of digestive enzymes
- explain the importance of microbes in digesting plant material
- compare the main features of the digestive systems of ruminants and hindgut fermenters.

1 The herbivores

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 'Plant Predators' on the DVD and read LoM Chapter 4. Unless stated otherwise, all the page references you encounter in this course will be to LoM.

In this section you are presented with information about the different groups of herbivorous mammals. Make a list of these groups, with the species in each group, in a notebook for reference. You can add more to the list as you continue to work through the course.

The plant predators, or herbivores, are a varied group, but they share certain characteristics. Many of them are large; among the smallest is the chevrotain (or mouse-deer) at about two kilograms weight, and the elephant is the largest, with a typical bull male weighing around six tonnes. Most herbivores can run fast and they usually have eyes at the sides of their heads, rather than at the front. These laterally pointing eyes provide wrap-around vision and enable them to feed while, at the same time, keeping watch for the animal predators that are likely to be a threat (the carnivores). For some, speedy locomotion enables them, more often than not, to make good their escape, as you will see towards the end of the TV programme 'Plant Predators'.

Most of these plant predators belong to a group generally referred to as the ungulates, whose identifying characteristic is that they have hooves, rather than claws. Within the ungulates, there are two orders, the odd-toed ungulates, or Perissodactyla, and the even-toed ungulates, the Artiodactyla. As you might guess, these groupings depend on the structure of their feet. The odd-toed ungulates are the horses and their relatives, like the zebras, with one toe, and the 'nail' modified as a hoof, and the tapirs and rhinoceroses which typically have three toes on each foot. You may already have spotted that there are some exceptions to these rules; the Brazilian tapir does have three toes on its hind feet, but its front feet have four - three functional ones plus a vestigial fourth toe. The even-toed ungulates have two or four toes, often with a gap between them, giving a cloven-hoofed appearance. They include the camels, deer, antelopes, cattle, sheep and goats. Additionally, included in this loose grouping of plant predators are the elephants, or subungulates, and the sloths, which belong to the order Xenartha.

In this course I'll be looking in more detail at some of the problems and consequences of adopting a plant-eating way of life, building on what you know already from reading LoM and watching the TV programme. As you know from LoM, the plants that make up the diet of many herbivores are grasses and broadleaved plants that are comparable in leaf structure to the familiar garden plants. Herbivores that eat grasses and other herbaceous (non-woody) plants are generally termed grazers and many of the animals I refer to in the early sections of this course are grazers.

2 The herbivore lifestyle - living on leaves

Leaves are a much less nutritious food than most kinds of animal material, so large herbivores have to eat large quantities of plants and they have special ways to digest their food. As author David Attenborough (DA) says, 'Leaves are extremely poor food' [p. 89]. To find out why living on a diet of leaves is particularly difficult, we need to know something about how leaves work.

Figure 1 shows a vertical section through a leaf, revealing the arrangement of the cells inside. Rather than providing a scale bar, here you will calculate the magnification and the size of the cells yourself. Since cells are very small, we need to use some very small SI units of length. The basic SI unit of length is the metre (m). One hundred times smaller than this is the centimetre (cm), and ten times smaller than that is the millimetre (mm). One thousand times smaller than that is the micrometre (μm, pronounced 'mew-em'). Cell dimensions are typically measured in μm.

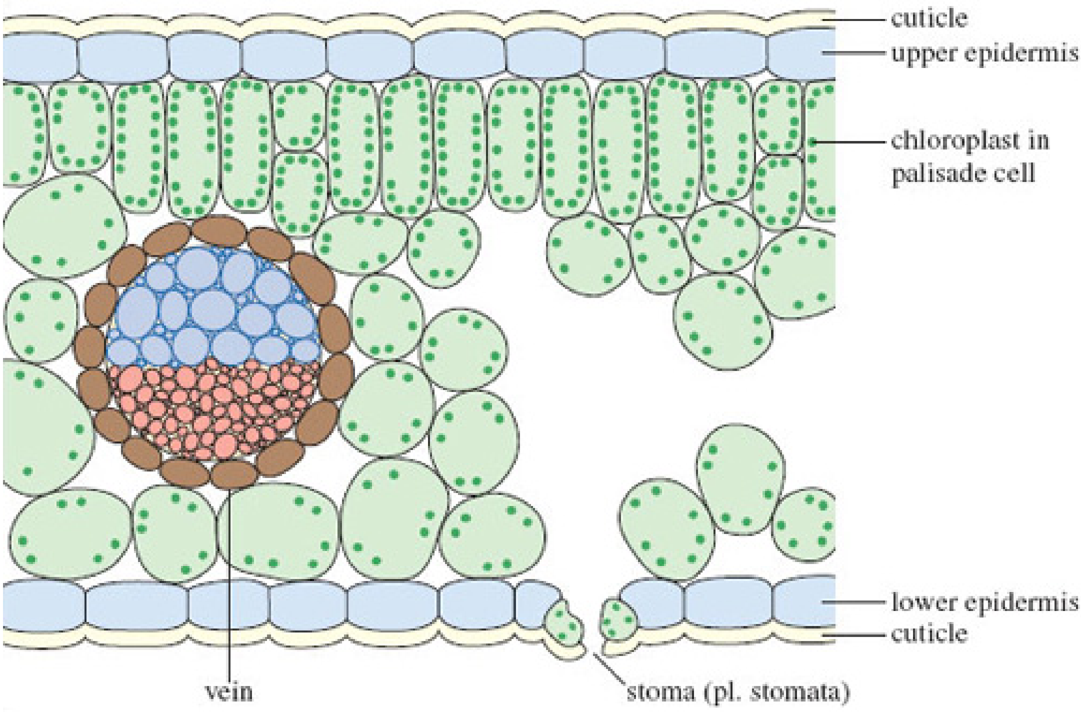

Figure 1 Diagram of a vertical section though a leaf. Both surfaces are covered by a protective cuticle, which reduces water loss from the leaf. Beneath the upper epidermis are the palisade cells, so called because they are lined up like the fence of stakes around a military establishment

Plants, unlike animals, can make their own food. The process by which they do so is called photosynthesis; 'photo' means light and 'synthesis' means building up. Plants harness sunlight as their energy source for the process that combines water (taken up through their roots) and carbon dioxide (taken in from the air through pores, called stomata, in their leaves) to make sugars.

Plants can use these sugars, together with minerals which are dissolved in the water in the soil, as the raw materials for all the other types of molecule that the plant needs for its healthy growth. A crucial role in photosynthesis is played by the green pigment, chlorophyll, which is located in tiny structures called chloroplasts, inside the cells of the leaf.

Activity 1

Watch the TV programme from 00.30-05.00, which includes sequences of the largest plant predator, the elephant, and one of the most unusual ones, the sloth, and then provides a look inside a leaf. It would be useful to make notes to help you identify the main problems that herbivores face. What does DA say is the main challenge of a green diet?

Answer

The main challenge is breaking the 'mesh of cellulose walls' which surrounds each plant cell, protecting the contents inside.

SAQ 1

Look at Figure 1, which shows how the cells are arranged inside a leaf. If in real life this leaf is only 1 mm thick, how many times is the leaf magnified in this diagram? How tall would one of the palisade cells actually be?

Answer

The leaf in Figure 1 is about 70 mm thick in the diagram, so it is magnified 70 times. One of the palisade cells is about 15 mm long in the diagram, so its actual size would be 15/70 mm or just over 1/5 mm. You can also express this as just over 0.2 mm or 200 μm (there are 1000 micrometres, μm, in a millimetre).

Each cell in the leaf is surrounded by a wall of cellulose. Chemically, cellulose is made up of strings of sugar molecules, joined together as threads, like strings of minute beads; these threads are criss-crossed to make a strong lattice around each cell. How can herbivores get access to the potential nutrients around and within the plant cells? Initially, plant material is subject to physical breakdown, grinding it up into small paricles using specially adapted teeth. This phase is followed by chemical breakdown of the cellulose lattice, to release the sugar molecules and allow access to the nutrients within the plant cells.

3 Herbivore teeth

Tables are a useful way of recording key information. The headings for Tables 1 and 2 have been prepared for you, and you can copy and complete the tables in your notebook. If you need to find any of this information again later, then it is very useful to have it summarised in a table.

If you are working through all the units in this series, you will recall the basic design and arrangement of mammalian teeth from course S182_2 *Studying mammals: the insect hunters*.

SAQ 2

Look back at Figure 2 in course S182_2. Which sorts of teeth would be particularly useful for biting off and chewing plant food?

Answer

Incisors could be used to cut off pieces of food (grass or leaves) and molars (and premolars) for chewing the food.

The molars of herbivores become worn down by constant grinding of plant material between them. The teeth are composed of softer and harder materials, notably dentine and enamel. The overlying enamel is a hard, resistant layer, especially important in the incisor teeth of rodents. When they first erupt, the molar teeth of herbivores often have an extra coating layer of cement (similar to the layer surrounding the root). So in herbivores, cement, enamel and dentine are worn down unevenly, such that differential wear usually produces ridges, especially in the molars and premolars, which make chewing more efficient. These cutting ridges of hard enamel are evident in a vertical section through the single functional molar tooth from the lower jaw of an elephant (Figure 2a, below).

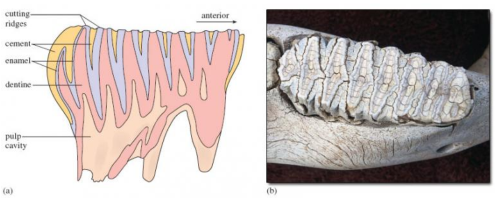

Figure 2 (a) Vertical section a single molar tooth of an elephant, with enamel ridges providing a serrated surface. (b) A view from above of the lower jaw of an elephant, showing a single molar. (To the left of this tooth, you can see a small part of the unerupted tooth behind, next in line to replace it.)

Figure 2a: adapted from: Hildebrand, M. (1974) *Analysis of Vertebrate Structure*, copyright © 1974, John Wiley & Sons, Inc. This material is used by permission of John Wiley & Sons, Inc.; Figure 2b: adapted from: Courtesy of Caroline Pond

Figure 2a: adapted from: Hildebrand, M. (1974) *Analysis of Vertebrate Structure*, copyright © 1974, John Wiley & Sons, Inc. This material is used by permission of John Wiley & Sons, Inc.; Figure 2b: adapted from: Courtesy of Caroline Pond

In all mammals, including ourselves, the molar teeth do not all erupt through the surface of the gum at the same time, but in mature adults all can be functional simultaneously.

SAQ 3

Reread LoM p. 29 and p. 122 to identify two very different herbivores that exploit this delayed eruption. Write a few sentences to explain how they do so, making clear the similarities and the main difference between them.

Answer

The two animals are the kangaroo, which is a marsupial, and the elephant, a placental mammal. In both of them, new molar teeth form at the back of the jaw and move forward to replace the old worn teeth, which then drop out. There are only limited numbers of teeth, so in each case, when all the teeth have been worn out, the elderly adults are unable to feed properly and starve to death. The main difference (apart from the fact that elephant teeth are much bigger) is that kangaroos have a total of only four pairs of molars on each jaw, whereas elephants have six pairs. Figure 2b shows a single elephant molar from above.

The ridges on the teeth of elephants and horses lie across the jaw, and the jaws move mostly backwards and forwards while chewing. Those on sheep and deer run from front to back, and the jaw movement is mostly side to side. You might be able to see this movement for yourself if you have the opportunity to watch some of these herbivores eating.

Activity 2

In LoM information is given about the diet and teeth of some other herbivores. Scan through the chapter then copy and complete Table 1 in your notebook using the headings provided below.

Table 1 Diet and teeth of a selection of herbivores

Name	Food	Teeth
tapir		
chevrotain		
rabbit		
hippopotamus		

Answer

Here is a completed version of Table 1.

Table 1 Diet and teeth of a selection of herbivores (completed)

Name	Food	Teeth
tapir	leaves mostly, but also fruits and nuts [p. 91]	two kinds of teeth: chisel-shaped incisors to snip off leaves; molars behind toothless gap, flat and ridged for grinding [p. 90]
chevrotain	fallen fruit and leaves [p. 94]	two teeth, one on either side of upper jaw, enlarged into short tusks [p. 92], molars [p. 94]
rabbit	mainly grass (and other herbaceous plants) [p. 95]	large pair of chisel-shaped teeth, with smaller pair at side [p. 95]

hippopotamus	grass (and other herbaceous plants) [p. 99]	Do not use teeth like conventional grazers (though their grinding molars are huge). Nip the grass with huge leathery lips, ripping up the leaves with sways of the head [p. 99]. The front teeth (i.e. the canines and incisors) have become tusks, used for display and fighting. Front incisors may be used for fighting, and thus become chipped [p. 102]

Now use the information you've entered in Table 1 to answer the following questions.

SAQ 4

Which teeth are missing in tapirs? Which other group of animals have you already met with a 'toothless gap' (scientifically it is called a diastema) and what did it enable them to do? (Check back to LoM p. 62 if you don't recall.) Do you think that the tapir's 'toothless gap' has a similar function?

Answer

Tapirs only have incisors and molars, so the canine teeth and premolars are missing. Rodents have a similar gap. This can be used to store the shavings of the coatings of the seeds on which many of them feed. Tapirs feed mostly on leaves, so probably their diastema performs a different function. It would allow food to be pushed between the upper and lower jaw through the gap, to be stored briefly in the cheek. Thus it is possible for the animal to eat more food without stopping to chew and swallow each mouthful.

SAQ 5

Teeth can be used for activities other than chewing. Which teeth are modified in the chevrotain and hippopotamus?

Answer

You probably correctly surmised that it is the canine teeth, which are enlarged into short tusks protruding from the upper jaw in the chevrotain, though it is not possible to see them in the LoM photograph [p. 95]. Canine teeth are used by carnivores for tearing off pieces of meat, but in herbivores these teeth are often used for other purposes. In the hippopotamus, both the incisor teeth at the front and the canine teeth, enlarged into tusks, are used for display and fighting.

Biting off and chewing up the plant material is the start of the process of breaking it down. These actions break the food into smaller pieces and squash the pieces to give a larger surface area for the chemical part of the breakdown, called digestion, to begin. The real process of extracting the nutritious material from inside the cells happens after the food is swallowed.

4 Digesting plant material

4.1 A brief digression about digestion

There are many new scientific terms introduced in this course. Are you making your own lists of them? If you were to encounter these terms in a fresh context (perhaps on a website, or during your own reading around these subjects), your aim should be not just to recognise the terms, but also to understand their meaning.

You will probably already know from the descriptions on food packaging that the important dietary components are protein, fat and carbohydrate, together with fibre, minerals, vitamins and water. You may already know the importance of the first three listed ingredients as sources of energy and as the constituent 'building blocks' for synthesis. The food that you eat, or that any mammal eats, has to be digested before the nourishment in it can be absorbed from the intestines into the bloodstream. The nourishment is then carried round the body in the blood to wherever it is needed for energy (mainly the muscles) or to where it is required to construct new body tissue or repair or replace worn parts. The process of digestion breaks down the molecules of protein, fat and carbohydrate into their building blocks.

The building blocks of proteins are called amino acids; they are joined together in long strings, which are broken apart when the protein food is digested. The amino acids are then absorbed and recombined inside the cells of the mammal's body in different, but very precisely determined, sequences to make different types of protein, including the 'structural proteins' that any particular species will need for its own muscle, skin, hair, etc. The order of the amino acids in the various proteins of the body is determined by the genes that the individual has inherited from its parents.

Fat is broken down into its two components (glycerol and fatty acids) which are absorbed into the bloodstream, and then may be reconstituted as fat when they reach the storage tissues of the body. Fat is mostly used to provide energy, and can be stored in various locations. If you have worked through course S182_2, you will recall the importance of fat cells (as WAT and BAT) and the role of the latter in arousal from hibernation.

Many carbohydrates are composed of strings of sugar molecules, so when they are digested, sugars are released, which again are primarily used to provide energy.

The process of chemically breaking down proteins, fat and carbohydrates is achieved by the action of enzymes.

SAQ 6

Where in the home might you come across a commercial product that contains enzymes, and what is the function of the enzymes there?

Answer

Biological washing powders contain enzymes, whose function is to break down food and other biological stains on the fabrics being washed. Meat tenderisers also contain enzymes, able partially to break down the proteins contained within the muscle and connective tissue (what we recognise as gristle) of the meat.

The great majority of enzymes are themselves protein molecules whose function is to speed up processes, such as digestion, which without them would go impossibly slowly. Just like the structural proteins mentioned above, enzymes have to be built up using the amino acids obtained from the breakdown of proteins in an animal's diet.

I've already mentioned that cellulose is the structural component of plant cell walls. It is a rather special type of carbohydrate, difficult to digest. In the human diet, cellulose is mostly considered to be 'fibre' or 'roughage', which passes straight through the digestive system, where it is important for the system's correct functioning, but provides no nourishment. Clearly, for a herbivorous mammal that eats only plant material, there must be a way to digest cellulose - and that is the topic of the next section.

4.2 Digesting cellulose

Figure 3 in this section contains a lot of information and many terms that are probably new to you. Set aside the detail for the moment, read the caption and try to get an overall impression. You should see that it shows the digestive systems of two herbivores, simplified and stretched out, rather than being folded up into the minimum space as they would be inside an actual animal. None of the other internal organs of the animals is shown. One of the great benefits of diagrams over photographs or accurate scale drawings is that in a diagram, you can just concentrate on the aspects you want to show and omit all other details. As you read the text, you will be introduced to different aspects of this diagram, so try to glance from the text to the diagram as you meet the various points.

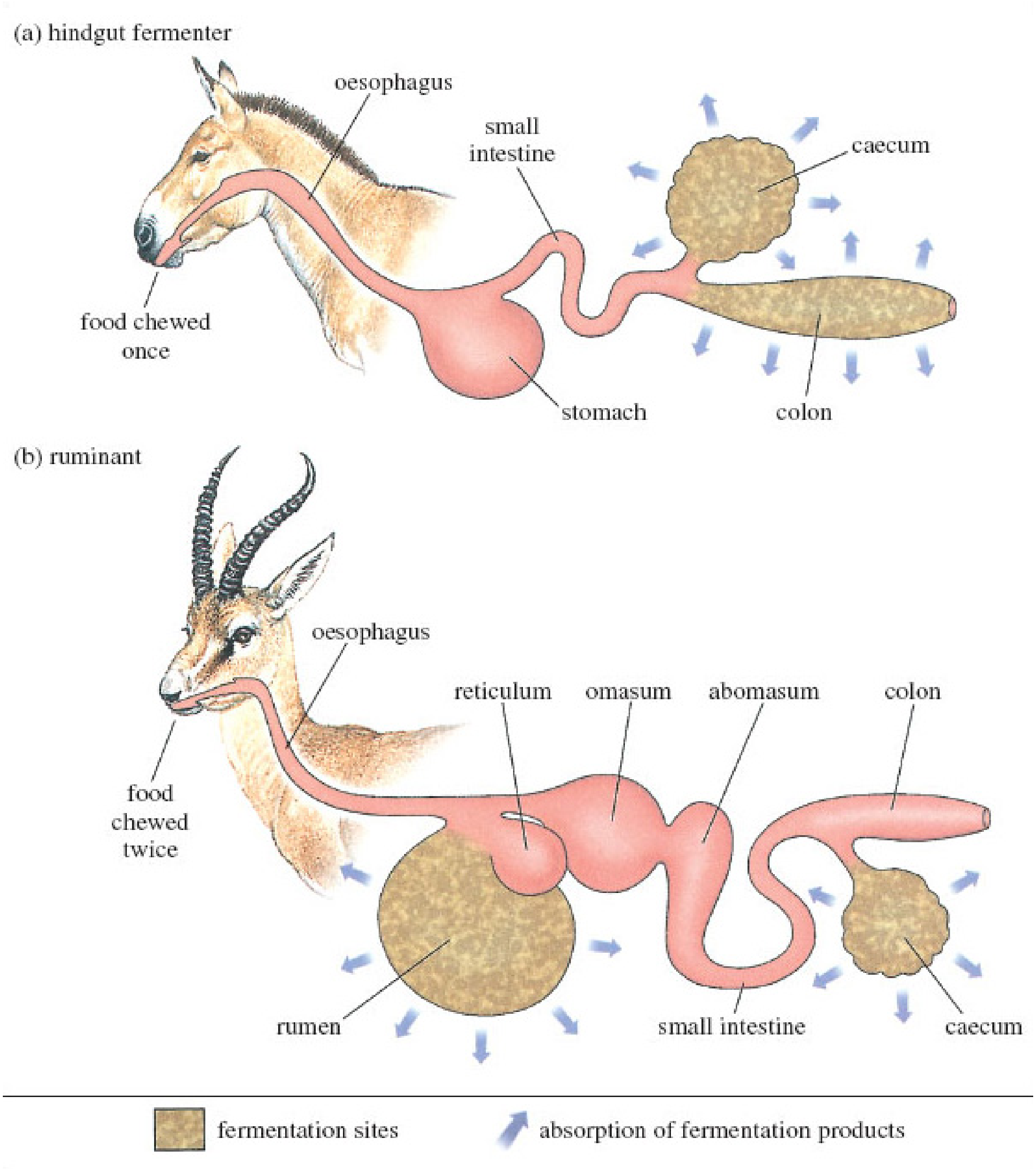

Figure 3 Simplified representation of the digestive systems of hindgut fermenters and ruminants

Figure 3: adapted from: Macdonald, D. (ed.) (2001) *The New Encyclopedia of Mammals*, Oxford University Press

Figure 3: adapted from: Macdonald, D. (ed.) (2001) *The New Encyclopedia of Mammals*, Oxford University Press

The enzyme needed to digest cellulose is called cellulase. Enzymes are often named like this, i.e. by taking part of the name of the substance that they digest and replacing the end of the word by '-ase'. For example, proteins are digested by types of enzymes called proteases and the sugar in milk, lactose, is digested by the enzyme lactase. Animals that live on plant material have detectable cellulase activity in their digestive systems. However, detailed genetic studies have shown that the vast majority of animals do not possess the gene for making cellulase, so the enzyme is clearly not synthesised by the animal itself. The gene for cellulase does appear to exist in a few animals, namely some insects (such as vine weevil larvae, cockroaches, termites and silkworms), some earthworms, a wood-boring clam, and a fish called the grass carp. This very odd assemblage of creatures has no close taxonomic relationship, indicating that the ability to produce cellulase probably evolved independently several times. Why it has not evolved more frequently is mysterious - it appears never to have evolved in mammals. Mammals that need cellulase have to make use of some additional species that do possess the gene - namely microbes, mostly bacteria and fungi, but also some protoctists (tiny organisms, most of them composed of just a single cell with a nucleus). Parts of the mammal's digestive system are modified to form large sacs where huge colonies of these microbes break down, or ferment, the cellulose.

SAQ 7

Most herbivorous mammals can be placed into one of two groups, according to where in their digestive system the cellulase-producing microbes are housed. Tapirs are members of one group and chevrotains belong to the other. From your reading of LoM, where are the bacteria found in each of these mammals?

Answer

The colonies of bacteria are in the hindgut of tapirs [pp. 90-91] and in the stomach of chevrotains [p. 94].

The two groups are known respectively, as the hindgut fermenters, for obvious reasons, and the ruminants, for reasons that are clear when you look at Figure 3.

SAQ 8

Look carefully at Figure 3 and use the information to write a few sentences in which you compare the location of fermentation and absorption in each type of digestion.

Answer

In both types of digestion, fermentation of the cellulose and absorption of the products occurs in two areas of the digestive system. The caecum (part of the large intestine) is used in both, but in hindgut fermenters, the second region is the colon, whereas in ruminants it is a special area of the stomach known as the rumen.

Activity 3

Now skim quickly through the whole of LoM Chapter 4 and complete Table 2, below, in your notebook with those animals you can identify as ruminants, those that are hindgut fermenters, and those whose digestive process you cannot be sure about at present. To avoid the lists becoming too long, you should group animals together where possible. You might like to complete the table in pencil, so that you can move animals from the 'Not known/other' column later if you find out more information about them.

Table 2 Preliminary list of herbivores using each digestive process

Ruminants	Hindgut fermenters	Not known/ other

Before you move on, compare your entries with the interim version of the table below. Read through the explanatory comments beneath that table. Remember to add to or change your own version of Table 2 as you work through the following text, which looks in more detail at these two types of digestion.

Answer

Interim version of Table 2 showing a list of herbivores using each digestive process

Ruminants	Hindgut fermenters	Not known/other
chevrotains	sloths*	rabbits**
deer, including caribou (reindeer)	tapirs	other lagomorphs [p. 95] and rodents
cattle	hairy rhinoceros	rhinos (black and white)
antelopes, including wildebeests	zebras and horses	hippos
gazelles		elephants
		camels

*In LoM [p. 89] we are simply told that the sloth 'maintains flourishing cultures of bacteria in its digestive system' but we are not told where. So you may have put sloths in the 'Not known' column. However, on pp. 90-91, the tapir and the sloth are said to both keep colonies of bacteria and other microbes in their hindgut, so sloths can be classified as hindgut fermenters.

**You were probably uncertain about rabbits, since we are told that they 'have their own particular way of digesting leaves. They eat their own droppings'. You may like to consider whether you think this is indicative of a ruminant or a hindgut fermenter.

A finalised version of the table is presented at the end of Section 5 (Table 3).

You may have been wondering how young herbivores obtain an initial colony of appropriate microbes. They are not, of course, needed for digesting milk - the diet of newborn herbivores. But during the weaning period, it appears that young animals ingest these microbes from the adults around them. They may do so accidentally by eating plants contaminated by adults' faeces. In some cases, it appears that the young deliberately eat the faeces of adults. This habit has been observed in elephants and, as you may have read in LoM Chapter 3 [p. 78], in the mole-rat.

5 Digestive processes

5.1 Ruminants

The earliest ruminant was probably an ancestor of the present-day chevrotain. The chevrotain skeleton appears to have remained virtually unchanged for the past 30 million years and, although there are now only four species confined to the jungles of Africa and Southeast Asia, they once had a worldwide distribution. So, chevrotains are placed in the suborder Ruminantia within the order Artiodactyla, to which other deer, antelopes, cattle, sheep and goats also belong. A second suborder, the Tylopoda, contains the camels and llamas; these also have a fermentation chamber within a complex stomach, and are therefore ruminants. So you can now transfer camels from the 'Not known' column of your Table 2 to the 'Ruminants' column. We'll be returning to camels later, too.

SAQ 9

What process is going on when an animal 'ruminates'?

Answer

When an animal ruminates, it retrieves lumps of its food from one compartment of its stomach, gives them a second chewing and then swallows them again into a separate chamber of its stomach where microbes continue to work on digesting the cellulose [p. 94].

The word 'ruminant' is derived from the Latin word *ruminare*, to chew again. To allow for the food to be chewed twice, the stomach of ruminants is complex, with four separate sections.

SAQ 10

Look again at Figure 3 and list the four sections of the stomach of a ruminant.

Answer

They are, in order: the rumen, reticulum, omasum and abomasum. (Technically speaking, only the abomasum is a true stomach; the remaining three sections are swellings of the oesophagus, which is the muscular tube that conveys food from the mouth into the stomach itself.)

When a ruminant is feeding, it does so in a series of quick bites, giving the food no more than a cursory chew between its molar teeth, mixing it with large quantities of saliva (several hundred litres per day in domestic cattle) and then swallowing it into the first of the chambers, the rumen. Here powerful muscles churn it with the microbes that start the fermentation process. The food ferments, generating methane and carbon dioxide which are eructed (burped!). The microbes start to break down the cellulose of the cell walls into sugars, thereby releasing other nutrients from inside the cells. The microbes use some of these nutrients for their own metabolism, and in doing so generate fatty acids, which the ruminant can absorb into its blood through the wall of the rumen and can use in its own metabolism. Large pieces of plant material float on top of the fluid in the rumen and are passed to the reticulum, which has honeycomb partitions in its walls. Here the food is formed into balls called 'cuds'.

Eventually the animal takes a break from feeding, selects a resting place where it can keep watch for predators and spends some time ruminating - the cuds are regurgitated and the animal chews the material again, mixing it with saliva and breaking it down into smaller particles. This process gives a bigger surface area for the microbes to continue digestion of the food when it is swallowed again.

Only when the material is very finely ground, does it pass into the omasum, where strong muscular contractions churn it up further. Finally, it enters the true stomach or abomasum, where the normal digestive enzymes get to work to break down the remains of the food and also to digest many of the microbes that have continued along with the food. Digestion continues in the small intestine, and absorption of the digested food into the blood begins through the wall of the small intestine. If any tough plant material has still not been broken down, there is a further opportunity for fermentation, and absorption in the caecum (the bulge from the side of the lower part of the digestive tract). Any material that still remains undigested is expelled from the body as faeces.

5.2 Pseudo-ruminants

Animals in the third suborder of the Artiodactlya, the pigs, peccaries and (according to most authorities) the hippopotamuses (suborder Suina), use a slight variant on the ruminant method, and are often referred to as pseudo-ruminants. You might like to add this information to your version of Table 2. These animals do have stomachs with several chambers, similar to the true ruminants, and the first of these chambers houses colonies of cellulose-digesting microbes. However, the pseudo-ruminants do not gain maximum benefit from this arrangement because they do not regurgitate the food and 'chew the cud'. So they are not able to extract as much of the nutrition from a diet of leafy plant material as a similarly-sized ruminant.

Pigs and peccaries overcome the problem by eating a varied diet, not exclusively composed of leafy plant material. As well as leaves and grasses, they eat fungi, ferns, roots, bulbs and corms, and fruit (all of which are easier to digest) and even some animals such as insect larvae, earthworms and sometimes small vertebrates like frogs and mice, which they come across while rooting in leaf litter and moist earth. The hippopotamus has evolved a different strategy to counterbalance its less efficient digestion - it reduces its energy expenditure.

SAQ 11

Reread LoM pp. 99-102 and note down the aspects of the lifestyle of the hippopotamus that reduce its energy expenditure.

Answer

Hippos spend their days wallowing in tepid, shallow water, so they do not need to expend energy in keeping warm. In fact, their cellulose-digesting microbes produce so much heat that these mammals risk overheating. The water supports the weight of their bodies and they generally move around very little in the water (though the one pictured on p. 100 is obviously on the move). So, during the day they expend little energy. Their main energy requirement is at night, when they climb out of the water to feed on grass on the riverbanks, travelling perhaps a few kilometres each night.

So hippos have a relatively inefficient digestive system, compared with true ruminants, but also have a low energy requirement. The herbivorous mammals that have taken the low-energy lifestyle to its extreme are, of course, the sloths. You might like to reread LoM pp. 87-90 to remind yourself about these animals (and perhaps watch them again in the first few minutes of the TV programme).

5.3 Hindgut fermenters

The odd-toed ungulates (comprising the order Perissodactyla), the horses, tapirs and rhinoceroses, are hindgut fermenters, as are elephants. Update Table 2 with this information. These animals have a relatively simple, small undivided stomach, but this time an even larger caecum and colon where the microbes are housed and where fermentation takes place, as you can see in Figure 3. One disadvantage of this method is that by the time the food reaches the caecum and colon, it has passed the main absorptive region of the gut (the small intestine) and so less absorption of the products of digestion is possible. Secondly, the large numbers of dead microbes also cannot be digested, as they can in ruminants, where they pass from the rumen into the small intestine with the remainder of the partly digested food. Here they are located in the part of the gut beyond the region of digestion.

Horses and their relatives overcome this situation in an ingenious way. Remind yourself of the position of the caecum as shown in Figure 3. It projects from the side of the gut, rather than being part of the main passage through. Food can therefore leave the caecum and instead of moving onwards into the colon, it can be moved back into the small intestine by reverse peristaltic movements (peristaltic movements are contractions of the muscles in the gut wall which propel the contents along). This process, known as intestinal reflux, allows further digestion and absorption to take place, before the food continues back again in its normal direction through the gut.

SAQ 12

Look again at LoM p. 96. Do you think that rabbits are hindgut fermenters? How do they gain the maximum nutritional value from their food?

Answer

Rabbits are indeed hindgut fermenters. The partly digested food, along with many of the microbes, is passed out as sticky black pellets, which are immediately eaten again, so that the material passes again through the digestive system. Further digestion and absorption can take place in the stomach and small intestine, and the material then bypasses the caecum on its second pass through, and is voided as the normal round rabbit droppings seen near their burrows.

Investigations show that this behaviour of rabbits, known as coprophagy, is common in other species of the order to which rabbits belong (the lagomorphs, LoM p. 95) and it has also been reported in rodents such as capybaras and coypus. Add these hindgut fermenters to complete your version of Table 2 and then compare it with Table 3, below.

Table 3 Final version of Table 2. List of herbivores using each digestive process

Ruminants	Hindgut fermenters	Other
chevrotains	sloths	pigs, peccaries and hippos (pseudo-ruminants)
deer, including caribou (reindeer)	tapirs	
cattle	hairy rhinoceros	
antelopes, including wildebeest	rhinos (black and white)	
gazelles	elephants	
camels	zebras and horses	
	rabbits and rodents	

6 Grazers and browsers

A good deal of the discussion so far has been related to animals that eat leaves in the form of grass and other herbaceous plants, the grazers, but this is not the only type of plant food. Also available as food are the leaves of trees and bushes. These form the diet of the browsers.

SAQ 13

There are some important differences between grass and other herbaceous plants as food and the leaves of trees and bushes as food. Consider two of these: (a) how much might be available in a given area; and (b) how they might each be affected by drought. Write a few sentences about each of these differences, on the basis of what you already know about grasses and suchlike and about trees with leaves, and from LoM and the TV programme.

Answer

(a) Grass tends to occur in large continuous expanses and grows close to the ground. Trees often occur in more scattered clumps and there may be some distance between one clump and the next. Also the leaves are at different heights above the ground, from low-growing bushes to tall trees.

(b) Grass (and other herbaceous) plants generally have short roots and so the growth is very dependent on the amount of water in the soil, and therefore on the local rainfall. If the soil dries up, the grass very soon withers and dies, though the roots probably remain viable in the soil, enabling the grass to regrow when the rains return. Trees, on the other hand, have deep roots which can obtain water from far below the surface and so some retain their green leaves for longer in times of drought and others are evergreen.

There are many types of tree in Africa that provide food for a variety of species of browser, of which one is the acacia.

Activity 4

Watch the TV programme again from 23.42-30.35 and make notes in answer to the following questions.

(a) Which animals are shown feeding on the acacia trees? Are they all competing for the same leaves?

(b) What is the likely benefit to the acacia of having these different animals browsing on its leaves?

Answer

(a) You should have observed a gazelle, called a dik-dik, feeding on the lowest leaves, then the impala (an antelope) feeding slightly higher up. Another antelope, the gerenuk, is able to stand on its hindlegs to eat leaves from nearer the top of the tree and, of course, giraffes can reach even higher. Elephants have the ability to stand on their back legs to reach high branches and they can use their bulk to push over the whole tree, so that they can browse on the leaves at the very top of the tree, which even the giraffes cannot reach. Thus five species are using the same tree for their food but each is eating the leaves at a different height.

(b) The acacia produces tough seed pods, which are eaten, but the seeds are not digested by the browsers. The seeds are deposited in their faeces at some distance from the parent tree, thus spreading the seeds across a wide area and allowing the acacia to increase its range.

Despite the seed-dispersal benefit, the acacia tree is under constant risk of losing its life-support, the leaves, which are vital for producing its own nutrients by means of photosynthesis. How plants protect themselves against attack by the plant predators is the topic of the next section.

7 Plant defences

Activity 5

Watch the 'Plant Predators' programme from 05.03-12.07 and make notes in answer to the following questions.

(a) In what ways do plants shown in this sequence protect themselves against their predators?

(b) How do tapirs avoid being poisoned?

(c) What is the purpose of the pika's haymaking activity?

(a) Plants may have spines and spikes on their leaves and stems (acacias have particularly fierce spines amongst their leaves, see Figure 4) and they may secrete poisons or have toxic chemicals inside their cells.

(b) Tapirs avoid being poisoned by being selective about the type of leaves that they eat and also by eating a mix of leaves, so that if poisons are present, they take in only a small amount of any one. They also seek out and eat quantities of a clay that is rich in kaolin [p. 91]. In their stomach, the kaolin binds to other chemicals, including any toxins which might be present in the food. (In humans, 'Kaolin and Morphine' preparations are still in occasional use as treatment for digestive upsets.)

(c) Pikas collect a variety of plant material, different sorts of leaves and flowers, and store it all in a 'hay pile'. By the end of the season, a pika may have amassed 30 kg of hay, some of it stolen from the haystacks of its neighbours (and from visiting TV presenters). Amongst the plants that pikas collect, there are some whose leaves contain poisons such as phenols that act as preservatives, so the 'hay' stays fresh for the pikas to eat over the winter period. Presumably, as with the tapirs, this mixed diet also means that pikas are unlikely to take in an 'overdose' of any one particular poisonous compound. Many other browsing species use a similar strategy, eating small quantities of a wide variety of plants, rather than stripping all the leaves from one species. And before we leave the subject of pikas, note that they are lagomorphs, and they too indulge in coprophagy. You might like to go back and add them to your completed Table 2.

Figure 4 Leaves and spines of the acacia tree

Figure 4: adapted from: Courtesy of Audrey Brown.

SAQ 14

Grasses have evolved some protection against their predators. What form does this protection take?

Answer

In many species of grass, there are tiny blades of silica (similar in composition to sand grains and glass) projecting from the edges of their leaves, which make the grass gritty and wear down the teeth of animals that eat it [p. 122]. As I mentioned earlier, the molar teeth of elephants are constantly replaced as they are worn down by chewing the food. For the same reason, horses have very long teeth, which emerge slowly, remaining about the same size as they gradually wear down with age.

8 Shortage of nutrients

8.1 Introduction

You know by now that plants can synthesise all the complex molecules that make up their tissues and seeds from very simple molecules - water, carbon dioxide and minerals from the soil. Mammals, on the other hand, need to take in many complex molecules ready-made, and some foods do not contain the right amounts or the right mix of nutrients. They have evolved various strategies to overcome the shortfalls, some of which are described in this section.

8.2 Protein shortage

Most plant leaves and stems contain very low levels of protein and so herbivores need to make maximum use of the amount available. You will recall that proteins in the diet are digested to amino acids, which are then absorbed into the bloodstream. Some of those amino acids are used to produce the mammal's own proteins (Section 4.1), but the proportions of different amino acids can be crucial. Most mammals are able to interconvert some types of amino acid into others, so the amino acids that are essential (i.e. have to be supplied in the diet) may be relatively few. Nevertheless, even in a diet low in protein, there are likely to be amino acids that cannot be used at that time and these extra ones cannot be stored. They must therefore be removed from the body. They are first converted by the liver into urea, which (in most species) is excreted by being dissolved in significant quantities of water and then passed out in urine. However, ruminants have a remarkable ability to recycle urea, via the microbes in their gut. The urea is extracted from the blood by the salivary glands and is reintroduced into the gut in the saliva. (You may recall from Section 5.1 that ruminants produce particularly large volumes of saliva.) The microbes use the urea to synthesise their own amino acids (a synthesis that mammals cannot carry out) and, when the gut microbes die, their proteins can be digested and used again by the ruminant. This recycling has another advantage for the ruminant: it reduces significantly the volume of urine produced and so conserves water.

SAQ 15

One ruminant derives particular benefit from this physiological adaptation, enabling it to survive on very little water *and* a low-quality forage. What is this mammal and what other special adaptations to desert dwelling does it display? (Reread LoM p. 103 if you need to refresh your memory.)

Answer

The animal is, of course, the camel. The special adaptations listed in LoM are:

- They can close their nostrils to keep out sand during sandstorms.
- They can eat dry, thorny vegetation that is inadequate to sustain most other large mammals.

- They can store fat in their humps to sustain them during periods of famine.
- Their droppings are very dry and their urine very concentrated.
- They can allow their body temperature to rise higher than in most other mammals before they begin to sweat.
- Their light-coloured fur reflects solar radiation, and also acts as an insulator, in this case reducing the amount of heat gained from the environment.
- They can live for up to two months without drinking.
- When they do drink, they can take in huge quantities of water - up to 120 litres at a time.

The contrast between the camel and other desert mammals is striking. Camels need to drink only occasionally, whereas desert hindgut fermenters, like asses, have to drink daily to take in enough water to make urine.

8.3 Shortage of minerals

You may be familiar with salt licks that are provided for domesticated cattle. In the wild, grass is also often low in minerals (e.g. it has almost no sodium and very little calcium), so grazers may have to go to extraordinary lengths to supplement their diet with additional minerals obtained from the most unlikely places. LoM gives some examples, but the most impressive activity takes place in the caves of Mount Elgon in Kenya [pp. 113-114]. You'll probably recall this spectacular footage from the TV programme (14.00-18.00), which showed bushbuck, buffalo and elephants in the cave, all obtaining salts from the cave. Indeed, elephants have an enormous requirement for sodium, having excavated many millions of tonnes of sodium-containing rock over a period of more than two million years. Sodium has a variety of important functions in the body, and in many herbivores - perhaps elephants included - it is thought to be especially important in the synthesis of chemicals that counteract the effect of ingested toxins.

9 Wildebeest migration

The skill of thinking in a scientific way is as much a part of being a scientist as is knowing facts - perhaps more so. In this series of units, you'll not only come across facts about particular techniques, such as radio transmitters and bat detectors, but also the *tactics* that scientists use to investigate problems. In this section, you learn about the importance of hypotheses and coming to logical conclusions. This way of thinking is hugely important in science, but it isn't the only way scientists operate and things are not always as logical and tidy as they seem here. How does this form of thinking differ from 'commonsense' approaches? Could the same approach be used to help explain other perplexing issues, such as the reasons for the zebra's stripes [p. 106]?

Activity 6

Watch the TV programme from 19.14-23.40 showing the huge numbers of animals, especially wildebeest, migrating across the plains of East Africa. There are some spectacular aerial photographs of this migration in LoM too [pp. 115-121]. What is the most obvious question to ask as you watch this compelling sequence?

Millions of animals undertake a dangerous journey of hundreds of miles between the Masai Mara in southern Kenya and the Serengeti to the south in Tanzania. The most striking question is why do they do it?

Possible reasons are given in LoM but an enormous amount of research has been done, starting in the 1950s, to reach these conclusions. Let us consider how this work might have progressed, to gain an insight into the way that scientific investigations can be carried out.

Imagine that you are a newly graduated biologist, with a particular interest in mammals, and you have been given funding to start to investigate the reasons for the wildebeest migration. How might you start the work?

You would first need to discover the details of the migration pattern, perhaps by following the animals in vehicles, or doing an aerial survey from a light aircraft or helium airship. You might also want to equip individual animals with small radio transmitters to follow their progress (radiotelemetry). (If you have been watching all the TV programmes in the series, you will recall from 'A Winning Design' that echidnas were fitted with similar small transmitters to enable them to be tracked.)

SAQ 16

Use the information in LoM p. 115 to write a couple of sentences describing the wildebeest migration. Remember, you are just reporting the observations on the migration pattern, not the explanation.

Wildebeest leave the grasslands of the southern Serengeti, Tanzania, in May at the start of the dry season and travel north to the grasslands of the Masai Mara in southern Kenya. When the rains begin again about six months later, the wildebeest return to the Serengeti.

Let us start with the first leg of the journey, from the Serengeti to the Masai Mara at the start of the dry season. It is relatively easy to come up with an explanation for this migration and you have read it in LoM. When the dry season begins, the grass on the dry (well drained) volcanic soils of the Serengeti begins to wither and the water holes dry up. So the wildebeest set off for the Masai Mara where occasional showers of rain allow the continued growth of grass and there is water to drink in the rivers.

However, it is much less obvious why wildebeest return to the Serengeti, just as the rainy season has returned and the grass is apparently growing really well in the Masai Mara. Let us assume that you have not read the explanation advanced in LoM, but that you are intrigued by this part of the migration and decide to study it further.

While making your observations on the migration, you might have thought of some ideas as to why the animals returned to the Serengeti. Such ideas, based on scientific observations, are called 'hypotheses'. A hypothesis can be defined as a tentative explanation, based on available evidence, which accounts for observations or facts. It can be tested by making further observations and then can be modified in the light of new evidence or observations.

Suppose that your hypothesis is that the wildebeest migrate to escape from their predators. Other work has shown that there are around 3000 lions and 9000 spotted hyenas living in the Serengeti and preying on herbivores like the wildebeest. During their breeding season, these predators need to remain close to their dens to feed their young and therefore it seems unlikely that they would follow the migrating wildebeest.

This hypothesis appears to be very reasonable and it was, in fact, one that scientists worked with for some time. It was supported by studies showing that wildebeest numbers were indeed less than the population size theoretically sustainable by the amount of available grass; so it seemed very likely that the numbers were being restricted by predators. However, it did not explain why other animals on the plain, which also fell prey to the lions and hyenas, did not migrate. Furthermore, studies of the hyenas showed that they would travel up to 60 kilometres from their dens to catch their prey, and so they could follow the wildebeest and continue to prey on them for a large part of their migration journey.

Eventually, therefore, this hypothesis had to be rejected since it no longer fitted the observations and facts, and another one had to be chosen and tested. Of course, in the real world of scientific enquiry, progress is not made in this linear fashion. Several groups of researchers are often working on the same hypothesis, collecting evidence which they may or may not share with one another, and other groups may be working on different hypotheses.

Returning to the wildebeest migrations, the hypothesis that has been under consideration for the longest time, is that food is the main factor. Clearly, because the wildebeest migrate away from the Masai Mara just as the grass is apparently at its best there, the hypothesis cannot be as simple as 'wildebeest migrate to where the grass is growing best'. Scientists therefore began to consider a more detailed hypothesis, that 'there is some specific feature of the grass that is different in the two areas and that affects the migration of wildebeest'. How could this hypothesis be tested? It needs some investigation.

SAQ 17

Imagine that scientists have collected fresh grass from the two areas grazed by wildebeest and returned quickly to their laboratory. What features of the grass might they examine?

Answer

They might look at the amount of energy available from the grass. They could measure the amounts of protein and minerals, to determine whether the samples from the two areas are equally nutritious.

In fact, this experiment has been done in a very systematic way. Areas in the Serengeti, the area to which wildebeest return in the wet season, and in the Masai Mara, the area where they graze in the dry season, were fenced off to protect the grass, and samples were taken twice a month. Concentrations of sodium, calcium, phosphorus and protein were checked, and measurements of the energy available were made. These values were compared with the minimum requirements to keep wildebeest healthy and to allow the females to produce sufficient milk for their young. The results showed that for most of the factors, the grass from either area would contain sufficient nutrients for wildebeest. However, in the grass from the Masai Mara, there was insufficient phosphorus in all the samples gathered, while phosphorus levels were above the minimum required in the grass from the Serengeti. Phosphorus (as phosphate) and calcium are essential constituents of bone. Other studies have shown that a lack of phosphorus in the diet of grazing animals, which can occur in cattle and sheep pasture in many parts of the world, results in bone and teeth abnormalities, as well as reduced fertility, slow growth, poor milk yield and increased mortality.

So, the hypothesis that 'there is some specific feature of the grass that is different in the two areas' has received support and can be modified to read 'there is a lack of phosphorus in the grass in the Masai Mara, which leads to a phosphorus deficiency in the wildebeest'. How might this revised hypothesis be tested?

An experiment would need to be set up to collect samples from individual wildebeest at different times of the year to measure the amount of phosphorus present in their bodies. Collecting tooth or bone samples could cause injuries to the animals, but blood and urine samples can be obtained from animals that have been mildly sedated. When this was done for a representative sample of wildebeest from the Masai Mara and from the Serengeti, it was found that the phosphorus levels in animals from the Serengeti were normal, but in animals from the Masai Mara were less than half the critical minimum levels. These data provide good support for the hypothesis - but we are still short of a link with migration.

Then scientists turned to the results of some other experiments. Sheep were experimentally deprived of phosphorus, which reduced their blood phosphorus levels to as low as those found in the wildebeest in the Masai Mara. These sheep were found to show a craving for bone and bird droppings and other natural sources of phosphorus. So there does seem to be a similar situation in which phosphorus deficiency leads to changes in behaviour. We can therefore modify our hypothesis to become 'migration in wildebeest from the Masai Mara is triggered by low levels of phosphorus in their blood'. So, it is now possible to begin to give an answer to question posed at the start - 'Why do wildebeest migrate?'

SAQ 18

Write a few sentences to explain the two parts of the wildebeest annual migration pattern.

Answer

Wildebeest migrate from the Serengeti to the Masai Mara at the start of the dry season, when the grass in the Serengeti dries up and water becomes scarce. The grassland of the Masai Mara is very low in phosphorus, so during the dry season, the wildebeest become increasingly short of this vital element. When the rains return, the wildebeest return to the Serengeti, where the grass has begun to grow again and contains much higher levels of phosphorus. The levels of phosphorus in their blood then return to normal during the wet season.

However there are still many unanswered questions - you may already have thought of some.

- Exactly how does the low level of phosphorus in the blood trigger the migration?
- How do the wildebeest know where to go to find grass with higher phosphorous levels?
- How do other mammals that do not migrate from the Masai Mara manage to survive on the low phosphorous levels available in the grass?

It's often said in science that answering one question does little more than raise a complete set of new questions and uncertainties, as is the case here. Only the passage of time (and the uncovering of more information) will reveal whether the 'phosphorus story' holds up to the scrutiny of future scientists, at which point questions like those above might be better resolved (while at the same time producing a host of new areas of ignorance).

10 Living in herds

Wildebeest are only one of the species of plant predator that live in herds. Many others do too.

Activity 7

Watch the the TV programme from 30.48-47.32 and read LoM p. 109. Identify and write down (a) a couple of advantages and (b) a couple of disadvantages of this sort of communal living.

Answer

(a) There is safety in numbers for the herbivores when there are carnivores around. Within a group of animals grazing together, there are a lot of eyes to spot an advancing predator and warn the others. Also, when the herd is running, it can be hard for a predator to single out a particular individual to attack. It may not be obvious where one animal ends and the next begins. Stripy zebras may be particularly tricky to separate.

(b) If food is short, living in a herd has its disadvantages. There are many other mouths competing for the same area of grassland or the same leaves on the trees. Living in a herd also complicates social life. There are many mature adult males and rivalry can lead to conflict and fighting between individuals, using a spectacular array of horns and antlers, as you will have seen towards the end of the programme.

However, since so many plant predators do live in herds, on balance it must be beneficial. If you are studying the next course in this series, you will be looking at the lives of some of those meat eaters that are dependent for their food on the plant predators, and at some of the consequences of living in groups that these carnivorous mammals face.

Conclusion

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