Studying mammals: Chisellers

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Introduction

All of the animals described in this course are members of the mammalian order Rodentia. The rodents are widely regarded as amongst the most successful of all the mammalian groups. We will examine some features of rodent biology that contribute to their success, in particular their exploitation of a unique range of plant foods, especially seeds, wood and roots. While focusing on rodent feeding behaviour and reproduction, we will also be exploring some more general ideas concerning the origin of the features that make an important contribution to rodent success.

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:

- explain the implications of a seed/nut-eating habit
- suggest why rodents are a successful order of mammals
- describe adaptation, based on knowledge of the theory of biological evolution by natural selection
- explain how altruistic characteristics can be understood in terms of kin selection and inclusive fitness
- give examples of the fitness costs and benefits associated with different reproductive behaviours.

1 The rodent

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 'Chisellers' on the DVD and read LoM Chapter 3. Unless stated otherwise, all the page references you encounter in this course will be to LoM.

At the start of LoM Chapter 3 you are immediately introduced to the importance of teeth for this group of animals. The 'chisellers' have the equipment to eat a very wide range of plant material, including leaves, bark, roots and seeds, and sometimes (as with beavers) wood itself. And as with other groups, their teeth are not used just for eating. They enable some members of the group to construct elaborate residences (the beaver's lodges, the mole-rat's underground caverns) and they can be used for fighting, as you can see on p. 78 in the photograph of two naked mole-rats squaring up to do battle.

All of the animals described in LoM Chapter 3 are members of the mammalian order Rodentia. The rodents are widely regarded as amongst the most successful of all the mammalian groups. They can be considered successful in terms of the number of species, comprising over 40% of all mammal species; most estimates nowadays are of the order of 2000 rodent species, and as the TV programme 'Chisellers' states, more than half (1300 by David Attenborough's (DA's) estimate) are loosely termed 'mouse-like rodents'. Rodents are also successful in terms of productivity: a single female Norwegian rat could have 56 young and over 400 grandchildren within 20 weeks of being born. And despite the fact that many of the photographs in LoM are delightful, this mammalian group is the one that many people would readily admit to disliking. Our dislike is perhaps partly rooted in the destruction that they wreak within our communities. It is estimated that 20% of the world's total food supply is either consumed or contaminated by rodents. Their role as carriers of pestilence, affecting both human societies and their livestock, has been understood and feared for many generations. It has been claimed that rat-borne typhus has single-handedly been responsible for more deaths than all the wars and revolutions throughout the history of humankind. But the war we wage against rats is singularly unsuccessful (they are notoriously difficult to poison) so it behoves us to learn more about this group, if only to enable our attempts to control them to be more effective.

In this course, I will examine some features of rodent biology that contribute to their success, in particular their exploitation of a unique range of plant foods, especially seeds, wood and roots. Seeds are rich in energy, but many roots and wood are tough and not very nutritious. Many seed eaters do not have to spend huge periods of time gathering their food, and so have time to spend ses001on other useful behaviours, such as reproduction. Whilst focusing on rodent feeding behaviour I will also be exploring some more general ideas concerning the origin of the features that make an important contribution to rodent success. To do so I will need to introduce you to important biological principles relating to evolutionary biology: natural selection and reproductive strategies.

2 You are what you eat

2.1 Overview

In this section, you will meet some new units, the units in which energy is measured. Nowadays, there are internationally agreed units (called SI units) that are often used in combination with a prefix to show the scale of the measurement. The SI unit for energy is the joule (pronounced 'jool', and with the symbol J) but from reading food packaging and books on diets you may be more familiar with measurements in the non-SI unit, the calorie (cal), or more usually the kilocalorie (kcal). Food labelling gives the equivalent in kJ as well, just as Table 1 does. 1 kcal is equal to 4.2 kJ (1 cal = 4.2 J). Notice that when you write a number with its units, you should always leave a space between the numerical value and the unit. Note too that the full names of most units begin with a lower case letter, but the abbreviation is an upper case letter; for example, 'joule' becomes 'J'.

Table 1 The energy yields of different nutrients

Nutrient type	Energy content	
	/kcal g^{-1}	/kJ g^{-1}
carbohydrate	4	17
fat	9	38
protein	4	17

The energy content of foods is assessed by igniting measured quantities of the foodstuff in oxygen and measuring the heat output.

In Table 1, the values in the columns give you the energy content of various sorts of food (carbohydrate, fat and protein) in kcal per gram and kJ per gram. But notice how 'per gram' is written as 'g^{-1}'. This representation is scientifically correct, but you will probably find it easier, at least at first, to continue to read 'g^{-1}' as 'per gram'.

You will have probably noticed too, that there is a division sign (/) before the units. Again, this is for reasons of mathematical accuracy. Consider the value for fat of 9 kcal g^{-1} (read as 'nine kilocalories per gram'). If we want to enter this in the table as just 9, then we have to divide the value by kcal g^{-1}. To show that all the values in that column are divided by kcal g^{-1}, the column headings are written as 'Energy content/kcal g^{-1}'. You will see the same representation in Table 2, where the percentages of various components of seeds are given and the columns are headed 'Water/%', etc.

I've already mentioned that rodents make use of a wide variety of foodstuffs, but both LoM and the TV programme emphasise the importance of seeds.

SAQ 1

There are problems inherent in using seeds as your main source of food. Both are described in some detail in LoM and the TV programme. In your own words explain the problem.

Answer

In a nutshell, the answer is that if you eat everything there is nothing for tomorrow.

Biting the hand that feeds you is one thing, killing it off quite another; clearly it is important that there is a balance between exploiting a source of food and destroying it beyond the point from which it can make a recovery. Relying on seeds is therefore a high-risk strategy because a seed cannot recover from being eaten; the only way the plant that produced the seed can reproduce successfully is by producing more seeds than can be eaten.

SAQ 2

On the basis of your reading of LoM, can you think of other hazards associated with specialising as a seed eater?

Answer

Few plants produce a continuous supply of seeds and in some temperate areas and desert regions the supply is seasonal.

The seasonal availability of seeds and the intermittent gluts associated with this seasonality were described at the beginning of LoM (p. 64, in particular). If you need reminding of some of the implications of a diet rich in seeds, reread Chapter 3 from the beginning to the end of the description of the marmot's behaviour on p. 67.

SAQ 3

The TV programme shows different rodents engaged in types of behaviour that get around the difficulty of using a source of food that is seasonal. Recall two of these behaviours.

Answer

(1) Storing or hoarding food. (This habit was also described in the section of LoM that you may have just reread.)

(2) Hibernating, having 'fattened up' during the season of plenty. This strategy is also described in LoM, for example in marmots [p. 67], which adopt a very different overwintering strategy to that of the much more continuously active beavers [p. 72].

As DA points out at the end of Chapter 2 [pp. 59-60], there can be costs associated with adopting a specialised diet. He described how the anteater's ability to eat ants and termites goes hand-in-hand with an inability to eat the wide range of invertebrates available as food to the non-specialist insectivores. In the sixth course in this series, S182_6 *Studying mammals: the opportunists*, we will return to examine this problem when we investigate the dietary choice of pandas. Despite the drawbacks of a specialist diet, we find that many rodent species do specialise in eating seeds, and the benefits of this habit are high because seeds are very nutritious.

SAQ 4

What is meant by 'nutritious'?

Answer

A nutritious food source is rich in energy. As DA puts it: 'seeds are particularly worth stealing for each is packed with … *energy-rich* food' [p. 61]. (The italics are mine.)

Bear in mind that nutritious food sources would also contain minerals and vitamins, in addition to energy-rich components. But in this respect, seeds are less beneficial; they have low amounts of the important minerals calcium and iron, for example, which are needed by rodents for the manufacture of bones and teeth, and blood, respectively.

SAQ 5

Study Table 1 in the box above. Which nutrient is the most energy-rich?

Answer

Fat, with an energy content of 38 kJ g^{-1}.

So does this measurement mean that seeds have a high fat content? Well some of them do (see Table 2 below) but, of course, the story is rather more complicated. There is the digestibility of the various dietary components to be considered, as well as the energy expended in obtaining the food. Gathering seeds from grasses and other types of plant may not be very arduous, but it is time-consuming; the TV programme 'Plant predators' contains some delightful sequences of pika rushing to and fro with swatches of grass, quite literally making hay while the sun shines. But grinding seeds such as grain is another matter, for it requires not only strength and stamina but also specialised equipment. When we look into the jaws of rodents, we generally find teeth that are highly specialised tools.

Table 2 Composition of some seeds (expressed as percentage by mass). These values are approximate and they ignore the other constituents (e.g. minerals and vitamins) present in comparatively small amounts.

Seed	Water/%	Protein/%	Fat/%	Carbohydrate/%
soya bean	7	38	24	31
sunflower	5	30	40	25
green pea	79	6	0.4	15
lentil	11	28	1	60
rape	2	28	35	35
ground nut	9	24	49	18
sesame	14	21	49	16
oats	9	12	9	70
maize	12	9	4	75
rice	12	7	1	80

wheat	12	12	2	74

2.2 Cracking nuts and other ways of eating

This section returns to the arrangement of teeth in the jaws of various mammals and uses the same representation for the dental formula as used in S182_2 *Studying mammals: the insect hunters*. You are not expected to remember the dental formulae of the various mammals.

We can tell a great deal about a mammal's diet, and therefore about its way of life, by studying its dentition. Before you study the armoury that enables the rodents to chisel into nuts, I'll remind you of the standard mammalian dental pattern and describe the differences found in rodent dentition.

Mammals have teeth of different types, differentiated from front to rear: incisor, canine, premolar and molar. (Where teeth are different in shape and size, the dentition is said to be heterodont.) For the hedgehog (see course S182_2) the dental formula is I3/2, C1/1, P3/2, M3/3. The pygmy shrew dental formula is different with respect to the lower incisors and premolars; I3/1, C1/1, P3/1, M3/3.

SAQ 6

What are the advantages of different types of teeth?

Answer

The differently shaped teeth are able to perform different functions. Incisors can nip or gnaw, canines can grasp, whilst molars and premolars shear and grind. Mammals have to process large amounts of food if they are to maintain their comparatively high body temperature and thus remain active. Having more 'tools' at their disposal gives the potential for more effective physical processing of food items before swallowing and 'handing over' to the digestive enzymes.

SAQ 7

The photograph of a Damaraland mole-rat [p. 76] shows the animal's incisors. How many incisors does the mole-rat possess?

Answer

The mole-rat has four incisors only.

SAQ 8

Apart from nipping off bits of tuber, how does the mole-rat use its incisors?

Answer

DA says that the mole-rat uses the front incisors 'not so much as chisels as mechanical excavators' [p. 76]. These little creatures excavate their way through soil and sand in search of a 'life-saving tuber' [p. 77].

All rodents are like the mole-rat and have only four incisors, two in the upper jaw and two in the lower jaw. As DA points out 'The wear on the incisors as they cut through the soil is particularly heavy, so it is essential that they grow fast and continuously. Consequently, the mole-rat's incisors have extremely long open roots that extend far back along the jaw, even beyond the roots of their cheek teeth' [p. 76]. These incisors are described as being rootless, as distinct from the rooted teeth described in S182_2. They retain the open pulp cavity with a good blood supply and so the teeth continue to grow throughout the animal's life. The action of opposing teeth as they gnaw and grind against one another gives the incisors chisel-sharp edges. As DA explains [p. 61], the incisor enamel is found only on the anterior (front) surfaces and enamel is harder than the underlying dentine, which consequently is more rapidly worn away on that side [p. 61]. The TV programme shows diagrammatically (at 02.52) how such sharpening is achieved.

Rodents have other distinctive dental features, also mentioned by DA. Canine teeth are entirely absent from the group. The gap between the gnawing front teeth and the chewing teeth behind is termed the diastema (Figure 1); when the lips can be drawn into this space, the mouth is effectively sealed off, so reducing the chances of swallowing any indigestible material gnawed off by the incisors. In some species the diastema provides deep pockets within which food can be temporarily stored during the to-and-fro shuttling associated with building up food hoards, an activity that is wonderfully illustrated in the TV programme. Many rodents have no premolars, though the molar teeth are often very substantial and sculptured in complex ways that promote the grinding up of plant material - features reminiscent of the dentition of the plant-eating mammals, which are highlighted in the next course in this series.

SAQ 9

To crack tough nuts, you need more than a chisel-sharp pincer action from teeth. What other features would be desirable?

Answer

Strong jaws and jaw musculature.

Figure 1 shows some features of rodent jaws and skulls and they indicate just how intricate the processes of gnawing and chewing in rodents are. The hinge of the jaw is complex. When the lower jaw is protruded forward, the incisor teeth engage, and can chisel or nip. In this position, the surfaces of the upper and lower teeth do not meet. But when the jaw slides backwards, the molars can grind the food, while the incisors hang over the lower ones, giving the animal the characteristic 'buck teeth' appearance.

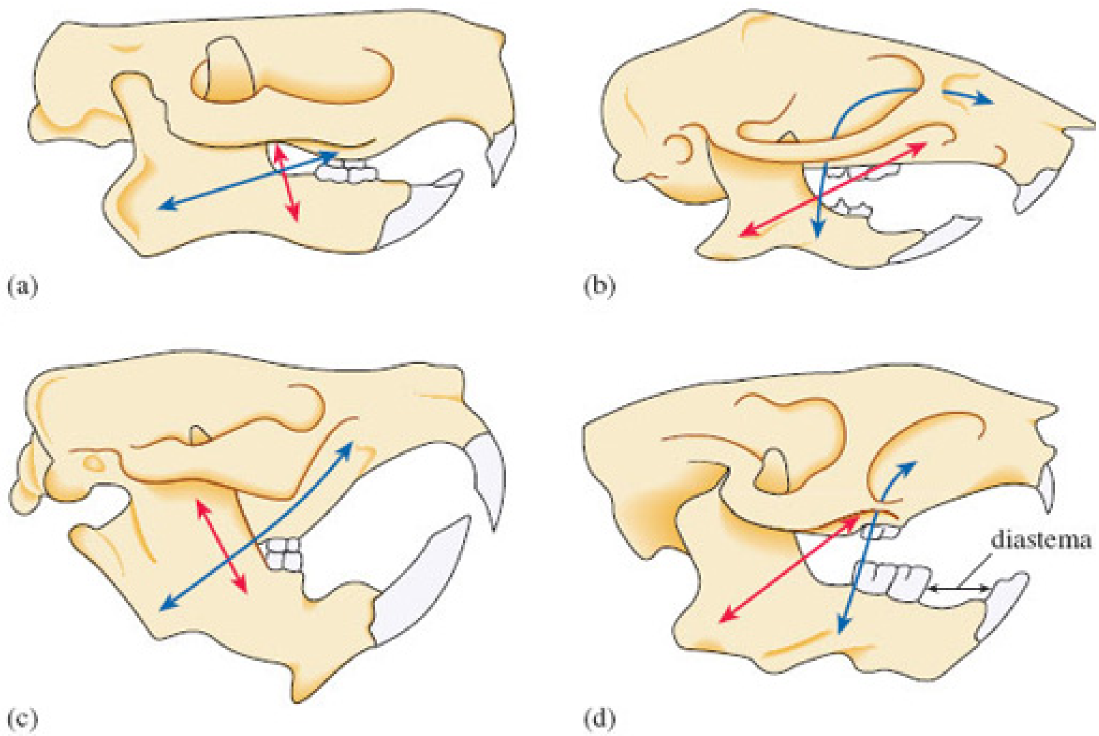

Figure 1 Some rodent skulls and jaws - the identity of each needn't concern you. Two sets of muscles, represented schematically in each case, are used for gnawing and for closing the jaw. (At one time, rodents were classified into three suborders on the basis of their jaw musculature.)

Figure 1: adapted from Young, J. Z. (1962) *The Life of Vertebrates*, Oxford University Press

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The muscles of the jaw are massive and are able to produce this backward and forward movement of the jaw. The major muscle is called the masseter, consisting of two main components, which are attached (i.e. inserted) at particular points in the upper and lower jaw. Figure 1a shows the arrangement typical of some types of squirrel, with points of insertion of these muscles drawn as arrow heads. That part of the masseter represented in red can close the jaw; while the masseter muscle shown in blue can pull the jaw forward. Figure 1b-c show the very different arrangement in other rodents and although the details needn't concern us, note that in rats and mice (Figure 1b), the insertion of the masseter is more forward onto the face, with one part of the muscle passing through the eye socket onto the muzzle. Note too that the lower jaw of many rodents has a large flange, where the masseter muscle is inserted. What these side views can't show is how the two halves (i.e. left and right) of the rodent lower jaw (the mandible) sit side by side. Rather than being fused, as with many mammals, these bones are linked by a ligament, a band of flexible tissue like a strap. This independent mobility allows the lower incisors to be brought together or pushed apart, facilitating manipulations such as prising open a nut. The teeth are firmly held in their sockets and not easily dislodged.

Activity 1

Watch 'Chisellers' on the DVD from 01.55-03.33 and 05.35-08.56, and compare the behaviour of squirrels and agouti as they eat nuts. Do you see any differences in the shape of their lower jaws, or in the musculature? What other manipulations are important for a successful nutcracker?

The feeding techniques involved are different, even to the naked eye. The agouti has a thickset head and a more massive jaw than the relatively delicate squirrel. The agouti holds the nut steady whilst the incisors gnaw persistently in one place. The squirrel appears to manipulate the nut so that a particular part of the surface can be attacked.

It seems then that a nut cannot generally be cracked unless it can be manoeuvred into the right position. You saw the squirrel using its forepaws to manipulate the white acorn before it started to gnaw; this was no random movement. As you know, the second programme extract in Activity 1 (05.35-08.56) was of a squirrel biting out the embryo before storing the remainder of the nut. Other research has shown that squirrels learn to gnaw along the weak 'seams' of a nut. Their proficiency improves with age - a result of learning, not just maturation. A squirrel reared on mashed food and not given the opportunity to handle nuts does not improve its handling technique with age.

3 Some principles that underpin evolutionary change

3.1 Introduction

Section 3 consists of several subsections of quite concentrated reading, describing some fundamental principles of biology. It shows how biologists need to use language very carefully and how commonly used words can take on a new and precise meaning. You will gain maximum benefit if you can read the whole of Section 3 in a single session, to follow the 'thread' that runs through it. In fact, you may find it beneficial to read this section through more than once, to satisfy yourself that you have a good understanding of the topic.

For the next part of the course, I'll be adopting a different and broader perspective. I want to introduce some underlying *principles* that you need to understand if the processes of evolutionary change discussed throughout this series of units are to make sense to you. LoM Chapter 3 and the TV programme provide a wealth of examples that illustrate my points. When I return to the main storyline again (in Section 4) the examples explored there are all the more meaningful if we follow an evolutionary perspective.

What you have been watching is the situation as it is today. However, the programme talks of 'an arms race' between plants and their predators and DA refers to plants 'strengthening the coats of their seeds', whilst mammals 'responded by developing powerful armour-piercing tools' [p. 61]. Whilst these shorthand ways of talking about evolution are commonplace, they are not accurate reflections of scientific understanding of the processes that underlie evolutionary changes. Scientists have to be careful that they express their understanding unambiguously. So in this section, I will show that scientists do not believe that these adaptations arise as a *response* to a challenging situation and explain why such a view of purposive change cannot be supported by scientific evidence or reasoning. I must first define adaptation and then consider the factors that *could* account for the evolution of protective seed coats and chisel-like teeth.

3.2 Adaptation

If you are working through the units in this series in sequence, you have already been introduced to the idea that many features of an animal's behaviour and structure are adaptations to their way of life. course S182_2 looked at the oily fur and the flipper-like feet of the water shrew, comparing the water shrew to the common shrew, a close relative that does not have these features and that does not chase prey under water. We also thought very carefully about the way that adaptations are described, taking care to avoid teleological explanations. In everyday speech we use adaptation to describe a deliberate modification; for example, I might describe a recipe as being an adaptation of one given to me by my mother. The Oxford English Dictionary suggests 'modifying' or 'making suitable for a purpose' would be correct usages, but it gives a different definition for biological usage.

Therein lies a problem frequently experienced by the student of biology; biologists take common words and then give them a new technical meaning. Worse is the fact that adaptation is a term that has more than one technical meaning. It can be used to describe the sort of responses that are transiently made to a novel situation. These behaviours can be learnt, such as a particular species exploiting a new food source, in which case I might say 'the marmot [p. 66] becomes adapted to a diet richer in flowers and leaves towards the end of the summer period'. Or the word might be used to describe a physiological response, such as an increase in metabolic rate in response to a change in T_a, in which case I might say 'the marmot adapted to a sudden cold spell by elevating its BMR'. Such events occur on a short timescale, within the lifetime of an individual. However, in what follows I'll be using the term to describe changes over a longer time period - indeed over an evolutionary timescale. Adaptations of this type have a genetic base and can be inherited.

> 'Adaptation is a central concept in most aspects of modern biology: however, like many powerful ideas, that of adaptation has been misinterpreted and misused.'
>
> (Evolution: a Biological and Palaeontological Approach, ed. P. Skelton)

> 'Adaptation … a complex and poorly defined concept.'
>
> (Evolutionary Biology, D. J. Futuyma)

Forewarned is forearmed! Clearly adaptation is an important but potentially tricky concept. The difficulty arises because the concept is at first glance absolutely straightforward, yet it is very difficult to demonstrate with scientific rigour. We can say that an adaptation is a biological characteristic of an organism that matches well with its natural environment. But how do we judge a good match when the organism's requirements and activities may change with seasons and with the stage in its life history, and when the environment around it is also constantly changing? One approach is to say that a characteristic is adaptive if the benefits it confers overall outweigh the costs. In practice, it is rather easier to seize upon obvious anatomical features and assign a beneficial function to them (e.g. the rodent incisors chiselling through nuts) than it is to subject our hypothesis to any test. Equally difficult might be the task of uncovering any negative aspects of the possession of such incisors (such as the fact that if an upper incisor is lost, the matching lower one continues to grow unchecked and grows into the skull of the animal).

So we have to be cautious when claiming that a biological characteristic is adaptive. For example, you might come across a reference to herbivores such as the gazelle having eyes that are set on the side of its head for good all round vision, an adaptation for a life lived in herds on the open plains. But if you work through the next course in this series and view 'Plant predators' (at 35:30), you'll see a gazelle spectacularly crash into a tree that it didn't see when trying to escape from a cheetah. A feature can be thought of as adaptive in one situation, whilst being a disadvantage at other times. We have to guard against drawing conclusions based on observation of only a small portion of an animal's life history. So, be prepared to be critical about how the term adaptation is used. For example, thinking of eyes on the side of the head exclusively as an adaptation for living in herds, implies that animals that don't live in herds wouldn't display this anatomical feature. But if things were that simple how might one explain (to give just two examples) the disposition of the eyes on the animals shown on pp. 64 and 80?

I'll leave the discussion there for the time being to talk more about how such adaptations as chiselling teeth could have evolved.

3.3 Variation

Fossil rodents are first found in rocks that date from around 65 million years ago (from the Eocene) and are thought to have evolved from insectivore/omnivore-type mammals that lived 100 million years ago (in the Cretaceous period). To say that they *evolved from* simply means that there probably is a direct line of descent but that the descendants have changed from their forebears. One of the most significant ways that evolutionary change can be brought about is by a process known as natural selection. This theory was first proposed by Charles Darwin in his book *The Origin of Species* in 1859. Darwin's book set out to show two things: that modern species had evolved from ancestral stock rather than having been divinely created, and that natural selection provides a mechanism whereby such evolution could have taken place. This theory has led many people to assume that natural selection is the only mechanism bringing about evolution. This assumption is not true. Random events, such as the eruption of a volcano or the strike of a meteorite, have made major impacts on the course of evolution. These momentous events take their place alongside less spectacular processes, such as genetic drift. Genetic drift occurs when, by chance, the frequencies of genes change in a population. But natural selection is the principal mechanism that can account for the extraordinary adaptations between prey and predators.

Many of Darwin's readers would have been familiar with the idea of selection because plant and animal breeders select individuals with desirable characteristics to be the parents of the next generation: strong, tough horses to pull the plough; sheep with fine-quality wool; high-yielding potato plants or attractive ornamental flowers. They then breed only from stock of the best quality. How could such a mechanism work in the wild? Darwin showed that there are a number of necessary conditions, of which the first is that there is inherited variation between individuals - even closely related animals living together.

SAQ 10

Take any mammal species with which you are familiar and list the kinds of variation that you see between individuals. (Don't forget that we are mammals too!)

Answer

I hope you have come up with a long list! If you thought of a domesticated species like dogs, cats or horses, you will have been aware of the artificial selection that has been applied (e.g. for body size and shape, coat length or colour). Your list will probably start with these anatomical features, but I expect you also thought of a number of physiological differences as evidenced, for example, by some seeming to need more food than others and some being more prone to disease than others. You might also have listed some psychological differences; some bold, others nervous, and so on. Next time you watch a *Life of Mammals* TV sequence, look out for individual differences. Probably most obvious are the fight sequences (see 'Chisellers' from 32.00-33.40), but watch the reactions of the baby Belding's ground squirrels diving into the burrow when the alarm is sounded. Some scampered off with alacrity; others were slower, taking a look around first. Which is the more adaptive response? A moot point!

So we can reflect that the individuals of a modern species are not all exactly the same and yet we might have suggested that they were all well adapted to their environment. For example, squirrels all have teeth that can chisel into nuts. Perhaps the differences are in other characteristics, ones that are not particularly important? Or maybe there are small differences between individuals in the quality of their teeth. My dentist used to tell my children that they were lucky to have inherited their father's strong teeth, and not my crumbly ones; maybe squirrels' teeth also vary in the hardness of the enamel! Darwin showed that even small, seemingly insignificant differences can become important when not all of the individuals can survive to breed - in other words, when there is competition between individuals for some of the resources necessary for their existence.

3.4 Competition

In plants it is particularly obvious that many more potential offspring (seeds) are produced than can survive. To a very large extent it is a matter of chance as to which are the survivors. Some are eaten, others overlooked or stored away and forgotten. Those that survive to germinate might be on unsuitable soil, too dry or too wet, so that they shrivel or rot. The successful seedling could be in poor soil, deficient in minerals, or there may be many other plants that are already established and blocking out the light, so preventing the seedlings from carrying out the vital process of photosynthesis. (This is the mechanism by which 'plants, fuelled by sunshine, can combine water, carbon dioxide and a few nutrients and so produce sugars and starches' [p. 61].) So survival is not always down to chance. Survival is sometimes achieved at the expense of others, or by being able to exploit a situation that others cannot. For example, a seedling with a physiological modification that makes it resistant to drought, or a seed with a slightly tougher, more waterproof coat that does not rot in the wet, may survive in conditions where others will die. Some nuts are not eaten because they are too tough and although the TV programme showed the agouti effortlessly chiselling through a large nut, personal experience with nutcrackers reveals that some nuts are harder than others and we, like the capuchin monkey, seen in the programme at 00.44, sometimes abandon the attempt to extract the kernel. A nut that survives this particular challenge, in theory, gets a chance to reach maturity. On the other side of the fence, the seed eater with slightly sharper teeth could use the nut that was discarded by its fellow. Having the edge over other individuals of your species makes a difference when resources are in short supply. The rodent with slightly sharper teeth or stronger jaw muscles might get through a hard winter because it could open all its stored nuts, whilst other less well-equipped individuals perish. In these circumstances we would draw the conclusion that the sharper teeth had given the animal a selective advantage. We could also reasonably claim that possession of these sharp teeth had been an adaptive feature.

The example above paints an extreme scenario. Much more subtle differences can confer advantage and the advantage may not make an immediately obvious difference to life expectancy. If one squirrel has a characteristic that enables it to make use of food that others discard, it could be better nourished itself and might also be able to rear more offspring. In the search for food, rodents compete with the farmer and they also compete with one another.

SAQ 11

If you have worked through the other units in this series so far, you'll have seen several examples of competition between individuals of the same species. Some of the most spectacular have been over access to females rather than food. Give some examples of competition between individuals of the same species.

Answer

Kangaroo (S182_1), shrews (S182_2), and marmots and capybara from this course. These were the examples that came to my mind, but you may well have noticed others.

All these examples show direct competition. There is direct physical interaction with a competitor. Other examples would include blocking access to food or water, as when a male lion chases younger members of the pride from a kill. Equally as important is indirect competition. Here there is no physical contact; instead, the successful competitor is one that is better able to utilise the resource that is limited, such as the nut discarded by others because it was too tough to crack. Many of these competitive characteristics are unseen. Examples include: being more resistant to infections; having a more efficient digestive tract or metabolism, so that you don't need as much food; or temperament - being bold or being nervous/timid - one can argue the case for either one being the more adaptive! So survival can be a result of successfully outcompeting the opposition. Yet what we judge as failure can be mistaken. In the programme 'Plant Predators' male topi antelopes fight one another and fall exhausted to the ground. In its last moments one individual is brought down and killed by hyenas. A fairly natural conclusion would be that here was an animal that had lost the struggle for existence, outclassed by other individuals.

SAQ 12

In the commentary, DA says that contrary to what this premature end might suggest, this topi's life had been 'a triumph'. By what measure was it deemed a success?

Answer

DA says the topi's life was a success because that season it had mated with a number of females in the previous few days.

Breeding is a biological measure of success; that one survives long enough to produce offspring that can themselves survive and reproduce. (Of course, we don't actually know about the abundance and fate of our topi's young, so it is a bit premature to declare his life a success!) The reason for this rather exacting measure of success is that many characteristics are passed down to subsequent generations by inheritance. If the topi was an exceptional beast, more efficient at obtaining and digesting food and more fearsome in fights than his rivals, but he spent all his time fighting and never got around to mating, then there would be no opportunity for these characteristics to be passed to succeeding generations. But if these characteristics have a heritable component and he breeds, and because of his superior powers he gains access to more females and breeds more frequently than his rivals, then his offspring will be numerous as well as being similarly advantaged relative to less efficient, less ferocious topi. Thus his offspring, in turn should have the opportunity to breed and leave relatively more progeny who also have inherited these desirable characteristics. Hence these desirable characteristics would come to be more widespread within the population. Of course, over a period of time the particular characteristics that advantaged the topi relative to others could become so widespread that they were possessed by all topi. When we can identify that such a change has occurred over time (e.g. from the fossil record), we demonstrate that evolution has occurred but we can only speculate on the role of natural selection as the mechanism.

3.5 Natural selection

Darwin summarised his theory of natural selection in the introduction to *The Origin of Species* as follows:

> As many more individuals of each species are born than can possibly survive; and as, consequently, there is a frequently recurring struggle for existence, it follows that any being, if it vary however slightly in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a better chance of surviving, and thus be *naturally selected*. From the strong principle of inheritance, any selected variety will tend to propagate its new and modified form. [The italics are mine.]

The important principle that Darwin first established here was that variation is quite separate from the direction of evolutionary change. Characteristics do *not* arise in response to an organism's needs. This notion is explored in course S182_2 where I draw attention to the way that statements implying a purpose for evolution are described as teleological and ought to be avoided. Doing so is by no means easy, for even the most respectable scientists and TV pundits use teleological statements to make points more forceably! But in my view there is a real danger that this practice will lead to misunderstanding of how natural selection works in those encountering these far-from-easy ideas for the first time. For instance, picking up the example I referred to earlier on, there is no 'arms race' in the sense of predator and prey actively involved in developing ever more cunning adaptations to outwit one another. Rather a variation that is 'in any manner profitable' can be naturally selected as individuals within a population come under pressure that affects their survival. The variant must already be in existence to be available for selection.

Yet we do see specific, reciprocal adaptations between species, eloquently described by DA [pp. 61-62 and pp. 122-123]. There are seeds that are protected from predators by their tough coats and, on the other hand, we find rodents with sharp teeth capable of cracking these tough nuts. The evolutionary processes that give rise to such specific forms of adaptation are called coevolution. In general, coevolution comprises a series of adaptive changes between two interdependent species, such that a change in one may, in time, favour the establishment of an adaptive response in the other. (Note this concept is very different from the one introduced in S182_2 as convergent evolution, where similar adaptations arise independently in unrelated organisms - e.g. the golden and marsupial moles.)

DA's account then goes on to give the vital clue that ought to alert us to the inappropriateness of the 'arm's race' analogy. He says 'So grasses have not only achieved a truce with those animals that feed on them' [p. 123].

How does DA's statement reveal the limitation of the 'arms race' analogy? In the human 'arms race' each side works to develop weapons of an increasingly destructive nature. In the natural situation, this kind of escalation would lead to the destruction, i.e. the extinction, of one of the species involved to the detriment of the other species. Instead of extinction, we observe that some species, especially pathogenic (disease-causing) organisms, show adaptations that allow coexistence. Much evidence from the long-term study of diseases shows that over time the pathogenic organism becomes *less* virulent. A much quoted example is the coevolution of the parasitic myxoma virus that gives rise to the disease of myxomatosis in rabbits. The virus is endemic in South America but the local rabbits do not usually die after becoming infected. When the disease was introduced into rabbit populations in Australia and the UK in the 1950s, it nearly wiped out the rabbit populations. Over the next few years after the population crash, rabbit numbers built up again as a consequence of both diminished virulence of the pathogen and increased resistance to the virus. Both organisms were observed to have changed. After the introduction of the virus, which is spread by biting mosquitoes, the rabbit population was reduced to a tiny percentage of its original size. 99.8% of the rabbits died.

SAQ 13

What reasons can you suggest to account for the survival of 0.2% of the rabbit population?

Answer

(1) These surviving rabbits might not have been infected with the virus.

(2) These rabbits might have had a natural resistance to the virus.

(3) These rabbits might have been infected with a less virulent form of the virus.

If the virus killed all the rabbits that it infected, it would not survive. There would be no means by which it could be transferred to the few uninfected rabbits. So if all the surviving rabbits were uninfected, we would have seen a subsequent build-up of the rabbit population but no evidence of the myxoma virus. Thus suggestion (1) cannot on its own account for the observed facts.

Both suggestions (2) and (3) are needed to account for the situation that we find today. They depend on there having been variation within both the pathogenic population and the rabbit population. In each case there was a very dramatic 'struggle for survival' - examples of indirect competition.

The story of the introduction of myxomatosis to these rabbit populations demonstrates natural selection at work. The selection pressure (the strength of selection) was very strong but you can appreciate that those rabbits who survived must have had a natural resistance to the virus. In the absence of the virus, this characteristic would have no particular value. Only with the introduction of the virus does the characteristic become adaptive. Such a characteristic is termed a preadaptation. A characteristic can only be designated a preadaptation with hindsight. The possession of a preadaptation is entirely fortuitous; selection cannot plan for the future. The outcome of the myxomatosis story was not predictable. Had there been no suitable variants, the whole of the rabbit populations in Australia and the UK would have been wiped out, as was the intention of those who introduced the virus.

SAQ 14

Can you now suggest one reason why it is difficult to poison rats?

Answer

There is variation in the rat population and if there are any rats that have a natural resistance to the poison they will survive and breed, while susceptible rats leave no offspring. The prodigious reproductive output of these resistant rats will ensure that numbers rapidly build up again and many of the offspring will inherit the characteristic that conferred resistance.

3.6 The numbers game … or the struggle for existence

In the majority of *The Life of Mammals* TV sequences there is relatively little evidence of any struggle for existence, apart from the occasional predator/prey interaction. Even then you are offered the comforting reassurance that 'four out of five chases end with the prey escaping'. So you could be forgiven for thinking that most mammals survive to a ripe old age, or at least until, like the topi, they have fulfilled their reproductive potential. Not so! Four out of five chases may end with the prey escaping, but that doesn't mean four out of five animals escape being eaten over a longer period of time.

But there is another, often more potent, threat to survival. One of the special characteristics of rodents that we drew attention to at the beginning of this course is their prolific breeding prowess. The calculation for the Norwegian rat in Section 1 demonstrated that the world would long since have been totally overwhelmed by rats if their numbers went unchecked! This prodigious ability to breed means that there is direct competition. Rats compete with other rats, mice compete with mice. A glimpse of the problem was revealed in the 'Chisellers' programme when we were shown a plague of mice.

Activity 2

Watch the TV programme from 40.20-41.42 and jot down any information on aspects of the breeding of the common house mouse. Compare what you learn of their behaviour with what DA describes towards the end of LoM Chapter 3 about population explosions in lemmings.

In cereal-growing areas in Australia, mice feeding on spilt grain in the field can invade grain stores, where the numbers proliferate rapidly, reflecting the enormous breeding capacity of these rodents. The economic consequences of such population explosions are clearly severe. The population explosions of the Scandinavian lemmings [p.85] occur under more natural conditions but have a less clear cause. They result in increased dispersion of the species, though no such benefit is as obvious from house mouse population explosions.

SAQ 15

In the TV programme we are told that females of the common house mouse can breed when they are five weeks old, and monthly thereafter. The litter size is between four and six. How does this compare with the Norwegian rat mentioned in Section 1?

Answer

Within 20 weeks of being born, the female Norwegian rat can have produced 56 offspring. The common house mouse can have had four litters in this time but, as it only has up to six young in a litter, it can (at most) produce 24 young after 20 weeks and so lags behind the Norwegian rat with its 56 young.

These vast numbers would not seem to be a good measure of success because so many of these creatures die. However, although I have already flagged the rodent's 'record-breaking productivity' [p. 84] as a feature that contributes to the rodent success story, I need to justify this claim that high productivity is an effective measure of success.

Large populations can be sustained if food is available for all, but the mice in the programme 'disappeared' once they had stripped the cornfields and the barns. As with the lemmings described in LoM p. 85, the population crashes - another example of the 'struggle for existence', as Darwin described it. Famine exerts a strong selection pressure on the rodents - few survive. We surmise that a mouse which survives, does so not by chance but because it possessed some variant of a character that was 'profitable to itself' (Darwin's words). For example, perhaps it could run further and faster than others to find food, or could survive on food that others found unpalatable, or had a better sense of smell and found food that others overlooked, or had sharper teeth and could break open nuts that others could not open. Whatever the detail of the character that confers advantage, the benefit of high productivity followed by a strong selection pressure is that the advantageous character can very rapidly increase in frequency within the population. Darwin saw that this mechanism suggests how new species could arise - a process called speciation. Indeed, it was this aspect that inspired the full title of the book *On the Origin of Species by means of Natural Selection, or The Preservation of Favoured Races in the Struggle for Life*. One measure of rodent success mentioned in Section 1 is the number of species. So, by this logic, the other criterion for success - productivity - could be responsible for the group's ability to have diversified and formed so many different species. When DA says at the end of LoM 'rodents are the most adaptable of mammals' you can now appreciate that he is not referring to an individual's behaviour but to the range of adaptations that are seen across the many rodent species.

My hope is that LoM and this series of units will give you an appetite to read beyond the materials supplied here. There is a wealth of high-quality popular books on evolution and natural selection, many of which describe Darwin's life and work. One of the best is *Almost Like a Whale* by Steve Jones, described as an 'update' of Darwin's *Origin of Species*. Reading it will give you a clear sense of why natural selection is regarded as such a fundamental biological concept. Another is *What Evolution Is: From Theory to Fact* by Ernst Mayr. Both books are available as paperbacks.

4 Individual lives: the concept of fitness

4.1 A measure of success

If what I have highlighted so far were the whole story, the only adaptive features shown would be those that equipped the rodent for times of famine, which is patently not the case. It is obviously a very important factor in the production of new species because the most productive of rodents (rats and mice) account for about 1300 of the 2000 or so rodent species, following the figures given in the TV programme. In LoM you have seen many interesting characteristics to which adaptive functions have been ascribed, but they are not all characteristics that enable their possessors to withstand famine. Day by day some animals die whilst others live because they were just a bit more effective in some respect, and it is only animals that survive long enough to breed that have a chance of passing on favourable characteristics to their offspring. In biological terms the individuals that have the greatest lifetime reproductive success relative to other members of the population are said to be the fittest. Here is another common word with a very particular biological meaning. Fitness is a measure of an individual's lifetime reproductive success relative to other members of the population.

SAQ 16

Thinking back to the discussion of the topi (Section 3.4), how would you define lifetime reproductive success?

Answer

The lifetime reproductive success of an individual is the number of fertile offspring that an individual produces during its lifetime *that survive to breed themselves*. (Remember that I said it was too early to judge the topi's life a success at the stage where he had merely mated with numerous females.)

Lifetime reproductive success in mammals is directly dependent on three factors.

1. The number of eggs or sperm produced.
2. The proportion of eggs produced that are capable of being fertilised and beginning development or the proportion of sperm cells produced that are capable of fertilising an egg.
3. The proportion of fertilised eggs that complete development and survive to reach breeding age themselves.

Lifetime reproductive success is indirectly dependent on the many characteristics that increase the individual's chance of surviving long enough to breed. Factors such as being alert and avoiding predation, being efficient at metabolising food and being resistant to disease can all contribute to lifetime reproductive success and hence to the individual's fitness.

Fitness is always measured *relative* to other members of the population so it is often called relative fitness. Although there is selection against the less fit individuals, the selection pressure against them may not be very strong. The fittest individual in a population might leave 50 offspring, whilst a less successful individual leaves 45. Both individuals have left many offspring and there is the chance of the balance altering in subsequent generations if the characteristic that gave the fittest animal the advantage happens to become less relevant. A good example from the TV programme arises from the handling of acorns by grey squirrels.

Activity 3

Watch the programme from 05.35-08.56 again and jot down some notes on the difference in timing of germination in red and white acorns and the effect this has on the acorn gathering by these grey squirrels. Then try and write an account (in about 100 words) of this phenomenon. Compare your response with what follows.

The acorns of red oaks don't germinate until the following spring, so are suitable for storage as they are. The white oak acorns normally germinate in the autumn, very soon after falling from the trees, so they are unsuitable for storage unless the embryo is removed - the germinating embryo would draw upon the stored nutrients (in this case, mostly starch) in the rest of the acorn, leaving nothing for the squirrel to eat. Squirrels can differentiate between the two acorns by smell; they store the acorns of red oaks but cut out and eat the embryo of the white oak before storing what remains.

Suppose a squirrel has a poor sense of smell and cannot reliably distinguish between the acorns from the red oaks and those from the white oaks. It might then store all the acorns it finds. Plentiful red oak acorns may have no negative consequences for the squirrel. Squirrels always store more than they need, so the loss to the squirrel of a few white oak acorns through their germination does not affect its ability to provision itself through the winter. However, if there is a poor crop of acorns from red oaks, then most of the squirrel's store is white oak acorns, which are of no use for the winter. This loss of red oak acorns may not be life-threatening, since squirrels eat other nuts and seeds as well, and insects (especially caterpillars) are a favourite. But the squirrel has wasted time and energy storing useless items, and its poor sense of smell means it will also be less good at finding hidden items of food stored by others.

You can see from what has been said that natural selection is not an all-or-nothing process. An individual that carries a few less favourable characteristics does not inevitably die young. The strength of selection varies. However, even very weak selection leading to a very small average difference in lifetime reproductive success will, if the selection pressure is maintained, result in a gradual increase in the numbers of the individuals with the more favourable characteristics as a percentage of the total population. In this way, through natural selection it would be possible for teeth that can chisel a hole in a Brazil nut to have evolved by a series of gradual changes.

4.2 Altruism

How is it possible then to sustain groups in which some individuals are prevented from breeding? They would have no lifetime reproductive success, none of their characteristics could be passed on to offspring.

SAQ 17

Name two of the species in LoM that had females in the group that were unable to breed or were prevented from breeding.

Answer

Marmot [p. 67]. Naked mole-rat [p. 78].

SAQ 18

What function is ascribed to the behaviour of the young female marmots?

Answer

They assist in keeping the burrow warm in the winter, enabling their mother's current litter to survive the sub-zero temperatures [p. 67].

Such a behaviour pattern, that benefits another individual at a cost to the performer's own individual fitness, is said to be altruistic. This is another word with a specific biological meaning that differs from lay usage and certainly does not have the same moral connotations.

SAQ 19

Is parental behaviour altruistic by this definition?

Answer

No, because the parenting increases the offspring's chance of surviving long enough to breed itself which, by definition, increases the parent's fitness.

In fact, careful thought shows that the daughter's non-breeding behaviour is not altruistic either because they are increasing the fitness of close relatives. A number of characteristics that have passed to them from their mother, and in particular the tendency to remain with her (which they can potentially pass on to their own offspring), are also passed to siblings and indeed are found in other close relatives. In such an instance, particular genes of an individual - genes being the factors that give rise to the characteristics in question - have been selected. But in this instance, an individual's behaviour has increased the chances of her *relative's* genes being carried into future generations - genes that the relatives are likely to have in common. Selection of this type is termed kin selection, and working to increase the fitness of your relatives benefits your own inclusive fitness. Inclusive fitness is your own lifetime reproductive success plus the lifetime reproductive success of related individuals that share, by inheritance, the altruistic characteristic.

SAQ 20

How long do the young marmots remain with their parents?

Answer

LoM suggests that the daughters only remain with their mother for a year [pp. 66-67]. DA says 'Marmots live in families of up to twenty individuals - a female and her mate, together with one or two young that were born at the beginning of the summer, and sometimes one or two of the female's sisters'. In the TV programme you saw that the young males leave home during the summer.

SAQ 21

What would happen to a young female that left home with her male siblings?

Answer

Any young female that left the group in the first summer along with the young males might mate and produce young, but without the warmth of the group of female bodies her young are more likely to die.

That is a strong selection pressure operating against the characteristic of 'running away from home in your first year of life'. However, the following year a group of young females, perhaps with one of their mother's sisters leave and form a new colony. For marmots, living in an extended family group in this way is not without its risks and costs - the amount of inbreeding (i.e. mating between closely related males and females) is known to increase but although in other species such a habit would lead an increased incidence of deformity and weakness, marmots for some reason seem to suffer no obvious deleterious effect. So the advantages of this form of group living must outweigh the disadvantages. Increased survival during hibernation apart, the origins of such 'staying at home' behaviour may reflect a severe limit on available new habitat - when suitable accommodation is at a premium, gaining social experience by remaining on home territory makes particular sense.

DA also describes the life of another rodent that lives in groups, Belding's ground squirrels. These animals live in much larger colonies than marmots for they are 'several hundred strong' [p. 74]. When foraging above ground they are vulnerable to predators but there are always some individuals on guard. 'But sentry duty is not shared by all. It is a dangerous job. … Matrons in this society, it seems, are more prepared than anyone else in the family to give their lives on behalf of the next generation' [p. 74].

SAQ 22

Why is it the females with young who are most prepared to take on sentry duty?

Answer

I am sure that you spotted that the chance of improving the survival odds for her offspring would be likely to benefit her inclusive fitness more than saving her own skin. Her offspring are younger than her, so they have greater potential to produce more offspring than she has.

You may wonder why the same argument doesn't show that the males should also take turns at sentry duty. To understand this paradox you will have to look a little more closely at the sexual habits of rodents.

5 Different reproductive strategies

5.1 Monogamy and polygamy

You've seen plenty of evidence that reproduction in rodents - more precisely what I've called their reproductive strategies - are versatile and varied. You'll appreciate that 'versatile and varied' describes the range of sexual habits seen in the rodents as a group, not the behaviour within a single species. As DA says, some are monogamous, which means that individuals mate exclusively with one partner, over at least a single breeding cycle or season. The marmots are an example of a group that practises monogamy. Some are polygamous in that individuals mate with several partners. Flying squirrels are polygamous, both males and females mate with as many partners as possible. Although this behaviour is sometimes described as promiscuous, it's best to avoid this term in a biological context because of its moral connotations. The term polygamous serves our purposes adequately. But the terms monogamy and polygamy should be used of individuals not of species. In some of those species where polygamy is observed, the behaviour is not possible for all individuals of the species. So you can talk of a polygamous individual, but not of a polygamous species.

Activity 4

In a few sentences describe the reproductive behaviour of the naked mole-rat and explain what is meant by the statement that 'polygamy is not possible for all naked mole-rats'.

(The reproductive behaviour is described on pp. 78-80.) Just a single female breeds in each colony, while her plentiful offspring comprise a number of discrete 'castes', such as workers, and dispersers. Many individuals do not breed at all at any time in their lives. It would not, therefore, be possible to describe these individuals as polygamous.

DA completes the description by saying: 'The reproductive system practised by naked mole-rats is a highly specialized one. No other rodent, indeed no other mammal does anything similar' [p. 80]. The colony structure and mode of reproduction in those mole-rats species that are highly social is indeed extraordinary. Figure 2 shows how the structure of such a colony and the variety of roles and activities evident have prompted some biologists to draw parallels between these rodents and the complex colonies of the social insects that you may have encountered, such as ants and wasps.

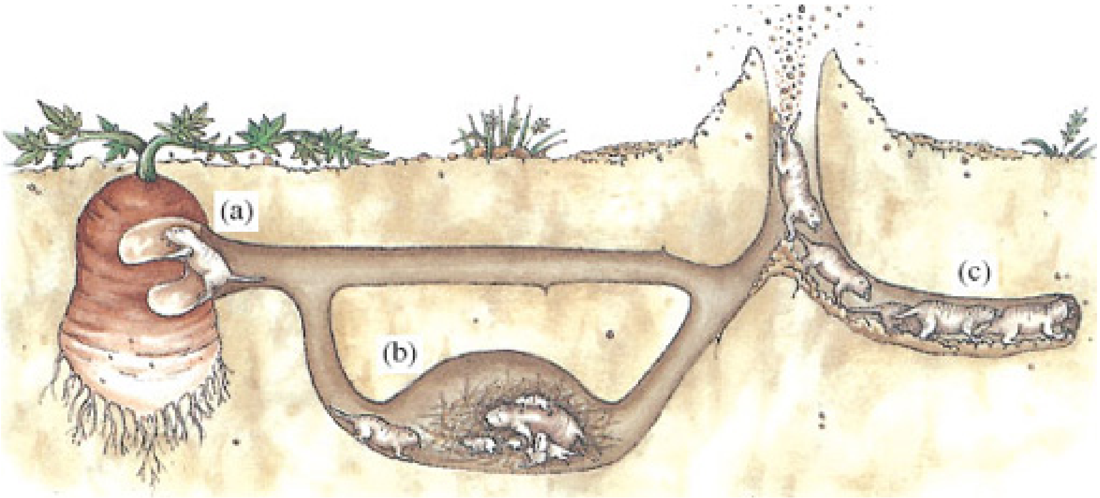

Figure 2 A typical burrow system of the naked mole-rat. (a) An individual is hollowing out a tuber. The central nesting chamber (b) is occupied by the breeding female, her offspring and 'subsidiary' adults. (c) A chain of workers involved in tunnel excavation.

Figure 2: adapted from Macdonald, D. (ed.) (2001) *The New Encyclopedia of Mammals*, Oxford University Press

Figure 2: adapted from Macdonald, D. (ed.) (2001) *The New Encyclopedia of Mammals*, Oxford University Press

The puzzling situation is why there should be a diversity of reproductive behaviour amongst rodents. Why is there not one 'best method'? Biologists propose two kinds of explanation. The first is the inequality of the sexes, and the second is the vagaries of the environment.

5.2 Differences between the sexes

In biology, 'sex' refers to a particular form of reproduction, sexual reproduction, that is distinct from asexual reproduction. As you know, sexual reproduction involves the production of eggs by females and sperm by males; eggs (or ova) and sperm are known as gametes. It is a universal feature of mammalian biology that in sexual reproduction there are two types of gametes and that progeny are produced by the fusion of two unlike gametes to form a single cell called the zygote. The zygote is the fertilised egg from which the young individual develops, passing through the blastocyst stage. Both partners to the sexual act make an equal contribution in terms of the amount of genetic material that the zygote receives.

It is a commonplace observation that half your genes came from your mother and half from your father. (This statement oversimplifies the issue, as you'll appreciate if you know of the distinction between alleles and genes; but for our purposes, the statement can stand.) What is not equal is the amount of effort that goes into the production of gametes. The eggs or ova contain more cellular material than the sperm; they are larger than the sperm. One consequence of there being two types of gametes is that, for a given amount of metabolic effort (i.e. internal synthesis), the female produces fewer gametes than the male. This fundamental difference between males and females means that a male's reproductive potential (that is the number of offspring he could potentially sire) is huge and he can improve his reproductive success by mating with many females. The female mammal is in a different situation.

SAQ 23

What factors limit the female mammal's reproductive potential?

Answer

Her reproductive potential is limited by the number of eggs she can produce. She cannot increase her reproductive potential by mating with many males. You probably also thought about the production of milk and how suckling her young would limit the number of potential offspring and hence the reproductive potential of a female. Clearly, reproduction requires a lot of effort for a female mammal. If she puts too much effort into the production and nurturing of her offspring at the expense of keeping herself in good condition, she may exhaust herself and be unable to breed again for a while, thereby limiting her reproductive potential.

A male mammal also puts effort into maximising his reproductive potential. However, we might expect that as a consequence of differences in male/female gametes, his efforts are focused on competing with other males for the possession of as many females as possible. I'm sure you can think of many instances, from the TV programme(s) in particular, where you have observed exactly this behaviour.

But contrary examples of animals may have sprung to mind. Why are they monogamous?

5.3 The effect of environment on reproductive behaviour

Activity 5

Review your reading of Section 4.2 on the family life of marmots (or reread LoM pp. 66-67) and construct an argument to explain why polygamy may not be profitable for the male marmot.

Answer

Your argument might run something like this:

- There is a short feeding season and the male marmot needs to lay down enough fat to last through the seven months of hibernation. Fighting other males uses up energy and feeding time.
- The family group defends its feeding territory from other families, so females are spread out over the alpine meadows. It would be difficult for one male marmot to control several female-centred families that were spread over a large area.
- If he was able to control several female-centred families, how could he prevent other males from sneaking into his territory and mating with a female that is some distance from him? The dominant female in a group 'bullies' the other females, they become distressed and abort. Therefore, it is only 'profitable' for a male to mate with the dominant female in a group; all other matings are wasted reproductive effort. How can he be sure he has mated with the dominant female and how can he be sure no other male has mated with her unless he has her near him all the time?

In terms of certainty of paternity we can already see reasons why a monogamous male marmot would be likely to leave more offspring than a polygamous male marmot. And so, as mentioned earlier, it is not just the differences between the sexes that determines the kind of reproductive behaviour we see in mammals, but also their habitat. Unless food is plentiful, the climate warm and predators few in number, the chance of a female successfully rearing young on her own is small. If males engage in parental care of the young they have fathered, they gain greater reproductive success than if they do not. In the case of the marmot community, parental care of so many infants through the long winter cannot be achieved by the two parents alone. Litter size can be maintained only by the recruitment of other females to the winter lodgings of the family. For many individuals, monogamy is the type of reproductive behaviour that has been determined through natural selection.

But monogamy is the exception amongst mammals. If you are studying all of the units in this series, in the next course you'll observe that many mammals are born relatively mature and 'ready to run', with a plentiful supply of food at their feet. These are the plant predators. You'll see plenty of examples of polygamous males putting their reproductive effort into courtship rituals: fighting other males and wooing females.

Conclusion

If you are working through all the units in this series, you'll be aware that this course has taken a somewhat different tack from earlier ones. I've used rodents to explore some fundamental biological principles that have a relevance far beyond this particular order. It is especially appropriate to talk about issues such as biological success in connection with rodents, given their very wide geographical distribution and the very large number of rodent species and individuals. You'll recall (from Section 4) that the family of rat/mouse-like rodents comprise more than 1300 species and new ones are constantly being identified. You've seen that many rodents are specialist seed eaters, gaining an energy-rich diet. They also have the opportunity for other behaviours, much of which is directed at reproductive effort.

You have also learnt a lot in this course about natural selection, which is the primary means whereby behaviour, anatomy and physiology can evolve and give us the adaptations that are so striking. Many such adaptations, as you've seen, are geared to the avoidance of famine, but others increase fitness in other respects. What you've seen is that the rodent body 'design' is a highly adaptable one. Think of rodents as different as naked mole-rats, beavers, maras, marmots and porcupines, all wonderfully described in LoM and shown in the TV programme. The lifestyles, behaviours and reproductive strategies of rodents are all highly adaptable features - the naked mole-rats, Belding's ground squirrels and maras, for example, testify to the marvellous variety of rodent 'family life'.

Rodent adaptations therefore comprise a wide range of structures, physiological traits and behaviours. In any particular rodent, such adaptive features are favoured by selection over and above alternative characteristics. (The distinguished evolutionary biologist Ernst Mayr defines an adaptation as any property of an organism believed to add to its fitness.) Keep in mind that natural selection only works on pre-existing variation. When you hear of the process of a mammal 'becoming adapted' to a particular environmental challenge, don't be seduced into thinking that adaptation is an active and directed process, as a relentless surge towards animal perfection. So, conjuring up a picture prominent in the next course, a lifetime of stretching of the giraffe's neck to reach the uppermost tips of the branches is not the way the structure became lengthened over evolutionary time. The fact that adaptations can be explained in ways that don't relate to an imagined 'will' or 'goal' of an animal, or to a lifetime's experience, make them no less remarkable.

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Figure 1 adapted from Young, J. Z. (1962) *The Life of Vertebrates*, Oxford University Press;

Figure 2 adapted from Macdonald, D. (ed.) (2001) *The New Encyclopedia of Mammals*, Oxford University Press.

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