## 2 Food and nutrition

## 2.1 **Introduction** The three main areas of wildlife management (conservation, sustained yield, and control) require knowledge of the food and nutrition of animal populations. Some of the important questions are:

1 Is there enough food to support and conserve a particular rare or endangered species?

2 What is the food supply needed to support a particular sustained yield?

3 Can we alter the food supply so as to provide more effective control of pest populations?

The field of animal nutrition covers subjects such as anatomy, physiology, and ecology, and there are several good reviews of these areas; for example, Hofmann (1973) deals with the anatomy of ruminants, Robbins (1983) addresses the physiology of wildlife nutrition, and Chivers and Langer (1994) review the form, function, and evolution of the digestive system in mammals. From the point of view of wildlife management, however, we are interested in two main types of information if we are to answer the preceding questions: we need to know (i) the availability of the food and (ii) the requirements of the animals. By matching the two sets of information, we can answer these questions. Sections 2.2-2.4 deal with availability, while Sections 2.5-2.9 address animal requirements.

## 2.2 Constituents of food

2.2.1 Energy

Energy is measured in units of calories or joules (1 cal = 4.184 joules). The energy contents of foods can be found by oxidizing a sample in a bomb calorimeter. Differences in the energy contents of different plant and animal materials result from the differences in their constituents. The energy contents of some common food components are given in Table 2.1. We can see that fats and oils have the highest content (over 9 kcal/g), followed by proteins (around 5 kcal/g) and then sugars and starches (carbohydrates; close to 4 kcal/g). The gross energy of a tissue depends on the combination of these basic constituents, particularly in animals. In plant tissues, energy content remains relatively uniform, in the region of 4.0–4.2 kcal/g. Plant parts with a high oil content, such as seeds (over 5 kcal/g), and evergreen plants with waxes and resins, such as conifers and alpine plants (4.7 kcal/g), are the exceptions (Golley 1961; Robbins 1983).

Energy flow through animals can be measured with isotopes of hydrogen (<sup>3</sup>H) and oxygen (<sup>18</sup>O) by the *doubly labelled water method* (Nagy 1983; Bryant 1989). First, water labeled with <sup>3</sup>H and <sup>18</sup>O is injected and allowed to equilibrate in the animal, this taking 2–8 hours depending on body size. A blood sample is then collected to establish the starting concentrations of the two isotopes. Analysis of <sup>3</sup>H is carried out by liquid

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Table 2.1Approximateenergy contents of foodcomponents.(Source: Robbins, 1983.Reproduced withpermission of Elsevier.)

Food Component	Energy (kcal/g)
Fat Protein Starch Cellulose Sucrose Urea Leaves Stems Seeds	9.45 5.65 4.23 4.18 3.96 2.53 4.23 4.23 4.27 5.07

scintillation spectrophotometry and that of <sup>18</sup>O by proton activation of <sup>18</sup>O to <sup>18</sup>F (the isotope of fluoride), with subsequent counting of  $\gamma$ -emitting F in a  $\gamma$ -counter. A second blood sample is collected several days later. The timing of the second collection does not need to be exact, but it should occur when approximately half of the isotope has been flushed from the body. Thus, timing depends on body size and the flow rates of the isotopes. Oxygen leaves the body via CO<sub>2</sub> and water, at a rate measured by dilution of the <sup>18</sup>O. Rate of water loss is measured from the dilution of <sup>3</sup>H. Thus, the difference between the total oxygen loss and the oxygen loss in water gives the rate of CO<sub>2</sub> production, which is a measure of energy expenditure. The method and its validation are described by Nagy (1980, 1989).

2.2.2 *Protein* The term *protein* covers a varied group of high-molecular-weight compounds; these are major components in cell walls, enzymes, hormones, and lipoproteins and are made up of about 25 amino acids linked together through nitrogen–carbon peptide bonds. Most animal species have a relatively similar gross composition of amino acids.

Animals with simple stomachs require 10 *essential amino acids*, these being the forms that cannot be synthesized by the animal and must be obtained in the diet: arginine, histidine, isoleucine, leucine, threonine, lysine, methionine, phenylalanine, tryptophan, and valine. *Nonessential amino acids*, therefore, are ones which can be synthesized in the body. Ruminants, as well as other species that rely on fermentation through the use of microorganisms, synthesize many of the amino acids themselves and so have a shorter list of essential amino acids.

Although there is some variability in the nitrogen content of amino acids (ranging from 8 to 19%), the average is 16%. Thus, in analyzing tissues for *crude protein*, the proportion composed of nitrogen is multiplied by the constant 4.25 (i.e. 100/16). The crude protein content of plant material tends to vary inversely with the proportion of fiber. Since one of the major constituents of fiber is the indigestible compound lignin, fiber content can be used as an index of the nutritive value of the plant food. In many plant tissues, such as leaves and stems, protein and digestible energy content (i.e. the non-fiber component) tend to vary together. However, some plant parts, such as seeds, are high in energy but quite low in protein.

2.2.3 *Water* The water content of birds and mammals is a function of body weight (W) to the power of 0.98 when comparing across species, but more restricted groups vary in the exponent. Robbins (1983) found the water content of white-tailed deer and several rodents varied as a function of W<sup>0.9</sup>.

Water is obtained from three sources:

- 1 Free water From external sources such as streams and ponds.
- 2 Preformed water Found in the food.

**3** *Metabolic water* Produced in the body from the oxidation of organic compounds. Preformed water is high in animal tissues such as muscle (72%) and in succulent plants, roots, and tubers. Because of this, carnivores may not have to drink often; herbivores such as the desert-adapted antelope, oryx, which eat fleshy leaves and dig up roots, can also live without free water (Taylor 1969; Root 1972).

The highest rate of production of metabolic water in animals comes from the oxidation (catabolism) of proteins, due to their initially high water content. Catabolism of fats produces 107% of the original fat weight as water, but the low preformed water content (3–7%) means that the absolute amount produced is less than that from protein (Robbins 1983).

Measures of free water intake from drinking underestimate total water turnover. More accurate methods use the <sup>3</sup>H or deuterium oxide isotopes of water: a known sample of isotopic water is injected into an animal, and after a period of 2–8 hours (depending on size of animal) for equilibration, a blood sample is collected; the concentration of isotope in the blood is then measured using a liquid scintillation spectrometer. A second blood sample is collected a few days to a few weeks later, again depending on body size, providing a new value of isotope concentration. Because water is lost through feces, urine, and evaporation, the isotope is diluted by incoming water. Therefore, the rate of dilution is a measure of water turnover. These techniques are described by Nagy and Peterson (1988) and have been used on a wide range of animals, including eutherian mammals, marsupials, birds, reptiles, and fishes.

2.2.4 *Minerals* Minerals make up only 5% of body composition but are essential to body function. Some minerals (roughly in order of abundance: calcium, phosphorus, potassium, sodium, magnesium, chlorine, sulfur) are present or required in relatively large amounts (mg/g) and are called *macroelements*. Those that are required in small amounts ( $\mu$ g/g) are called trace elements (iron, zinc, manganese, copper, molybde-num, iodine, selenium, cobalt, fluoride, chromium). So far, very little is known about the mineral requirements of wildlife species, but Robbins (1983) has provided a summary of available information. It is assumed that most native species are adapted to their environment and so can tolerate the levels of minerals found there (Fielder 1986). However, some mineral deficiencies have been observed. Selenium deficiency increases the mortality of juvenile, preweaned mammals (Keen and Graham 1989). Flueck (1994) supplemented wild black-tailed deer in California and increased preweaning fawn survival threefold.

Calcium and phosphorus are essential for bones and eggshells. Cervids have a very high demand for these minerals during antler growth. Calcium is also needed during lactation, for blood clotting, and for muscle contraction. Phosphorus is present in most organic compounds. Deficiencies of calcium result in osteoporosis, rickets, hemorrhaging, thin eggshells, and reduced feather growth. Carnivores that normally eat the flesh of large mammals need to chew bone in order to obtain their calcium. Mundy and Ledger (1976) found that the chicks of Cape vultures (*Gyps coprotheres*) in South Africa developed rickets when they were unable to eat small bone fragments. This has an important management consequence: bone fragments from large carcasses are made available to vultures by large carnivores, in this case lions and hyenas; where

carnivores are exterminated on ranch land, carcasses are not dismembered and bones are too large for the chicks to swallow. This is a good example of how the interaction of species should be considered in the management and conservation of habitats.

Sodium is required for the regulation of body fluids, muscle contraction, and nerve impulse transmission. Sodium is usually found in low concentrations in plants, so herbivores face a potential sodium deficiency. In areas of low sodium availability, herbivores consume soil or water from mineral licks (Weir 1972; Fraser and Reardon 1980). Carnivores can easily obtain sodium from their food, and so are unlikely to experience sodium deficiency. Isotopic sodium has been used as a measure of the food intake rates of carnivores such as lions (Green *et al.* 1984), seals (Tedman and Green 1987), crocodiles (Grigg *et al.* 1986), and birds (Green and Brothers 1989). This approach is possible because sodium remains at a relatively constant concentration in the food supply. The technique is similar to that for isotopic water described in Section 2.2.3.

Both potassium and magnesium are abundant in plants, and deficiencies in free-living wildlife are therefore unlikely. The same is true for chloride ions and for sulfur. Trace element deficiencies are unusual under normal free-ranging conditions but they occur locally from low concentrations in the soil: there are some reports of iodine and copper deficiencies and of toxicity from too much copper and selenium (Robbins 1983).

2.2.5 *Vitamins* Vitamins are essential organic compounds that occur in minute amounts in food and cannot normally be synthesized by animals. There are two types of vitamin: fat-soluble (vitamins A, D, E, and K) and water-soluble (vitamin B complex, vitamin C, and several others). Fat-soluble vitamins can be stored in the body. Water-soluble vitamins cannot be stored and hence must be constantly available. Overdose toxicities can arise only from the fat-soluble vitamins.

Vitamin A, a major constituent of visual pigments, can be obtained from  $\beta$ -carotene in plants. Vitamin D is needed for calcium transport and the prevention of rickets. Vitamin E is an antioxidant needed in many metabolic pathways; it is high in green plants and seeds, but decreases as the plants mature. Vitamin K is needed to make proteins for blood clotting. Deficiencies are unlikely to occur because it is common in all foods. The vitamin K antagonist, warfarin, causes hemorrhaging. It is used as a rodenticide.

Little is known about the B-complex vitamins and whether deficiencies occur in free-living wildlife species, although cases of thiamin (B1) deficiency have been reported for captive animals (Robbins 1983). Vitamin *C* differs from the others in that most species can synthesize it in either the kidneys or liver. Exceptions include primates, bats, guinea pigs, and possibly whales. Vitamin *C* is not as commonly available as the B vitamins but is found in green plants and fruit. It is absent in seeds, bacteria, and protozoa.

Other physiological constraints that may not be called vitamins nevertheless provide limits to animal nutrition. For example, old-world starlings and flycatchers cannot digest sucrose (Martinez del Rio 1990).

# 2.3 Variationin food supply2.3.1 Seasonality

Food supply varies with season. To some degree, all environments are seasonal, including those of the tropics. Food supply is greatest for herbivores when plants are growing: during the summer at higher latitudes (temperate and polar regions) and during the rainy season in lower ones (tropics and subtropics). Protein in grass and leaves declines from high levels of 15-20% in young growth to as little as 3% in mature flowering grass,

or even 2% in dry, senescent grass. Leaves from mature dicots maintain a higher protein content of about 10%. Thus, herbivores such as elk in North America and eland and elephant in Africa will switch from grazing in the growing season to browsing in the non-growing season. Many forest-dwelling Australian marsupials are mycophagous; that is, they prefer to feed on the sporocarps of hypogeous fungi. They feed on dicot fruits and leaves when fungi are about. Growth rates of pouch young in the Tasmanian bettong (*Bettongia gaimardi*) are directly related to periods of sporocarp production (Johnson 1994).

Winter is the main period of stress for animals in higher latitudes. Low temperatures create higher energy demands just when energy is less available. For example, energy intake of moose in Norway declines by 15-30% during winter, resulting in a deficiency of 20-30% relative to their requirements. Energy intake is less (573 kJ/kg<sup>0.75</sup>/day) in poor habitats than in good ones (803 kJ/kg<sup>0.75</sup>/day) (Hjeljord *et al.* 1994). Even greater reductions in food intake rates during winter have been recorded for black-tailed deer (Gillingham *et al.* 1997)

Animals adjust their breeding patterns so that their highest physiological demands for energy and protein occur during the growing season. Thus, northern ungulates give birth in spring so that lactation can occur during the growing period of plants, whereas tropical ungulates produce their young during or following the rains, allowing the mother to build up fat supplies to support lactation. Although most birds complete their entire breeding cycle during one season, the timing of breeding is closely associated with food supply (Perrins 1970). Very large birds such as ostrich behave like ungulates and start their reproductive cycle during one wet season so that the precocial chicks hatch at the start of the next (Sinclair 1978).

Carnivores also adapt their breeding to coincide with maximum food supply. Thus, wolves that follow the caribou on the tundra of northern Canada have their young at the time caribou calves are born. Schaller (1972) records that lions on the Serengeti plains of Tanzania have their cubs when the migrant wildebeest are giving birth. In the same area, birds of prey have their young coinciding with the appearance of other juvenile birds and small mammals, which form their prey (Sinclair 1978).

A particular kind of variability in food supply occurs with the production of prolific seed crops by some tree species. This seed is termed *mast*. It occurs when the majority of trees in a region synchronize their seed production. Beech trees (*Fagus*, *Nothofagus*) and many northern-hemisphere conifers (e.g. white spruce, *Picea glauca*) produce their seeds at the same time, these mast years occurring every 5–10 years. Birds that depend on these conifer seeds, such as the crossbill (*Loxia curvirostra*), breed throughout the winter when a mast cone crop occurs. In the following year, when few cones are produced, the crossbills disperse to find regions with a new mast crop, sometimes travelling many hundreds of kilometers (Newton 1972).

Red squirrels (*Tamiasciurus hudsonicus*) also respond to cone masts in white spruce. This species caches unopened cones in food tunnels in the ground and uses them throughout the next winter. Survival of squirrels is high during these mast winters.

An unusual form of variability in food supply occurs in the bamboo species that form the main food of the giant panda (*Ailuropoda melanoleucus*): the bamboo synchronized flowering in much of southern China during the early 1980s (Schaller *et al.* 1985) and then died, and there was little food available for a few years. With the giant panda now confined to a few protected areas, the population suffered from this sudden drop

2.3.2 Year-to-year variation in food supply

in food supply. Knowledge of such events is important for conservation. It tells us that reserves must be sufficiently diverse in environment, habitat, and food species to avoid the type of restriction in food supply produced by the synchronous flowering of bamboo. Presumably in prehistoric times giant pandas were able to range over a much wider area and so take refuge in regions where bamboo was not flowering. They cannot now move in this way and most of their former range in the lowlands is no longer available.

In the Canadian boreal forest, lynx and great horned owls breed prolifically during the peak of the 10-year snowshoe hare cycle and cease breeding during the low phase (Rohner *et al.* 2001).

Many plants produce chemicals that deter herbivores from feeding upon them. These chemicals are called *secondary compounds*. Their production is associated with growth stage, but this association differs between plant species. Although secondary compounds are found in some grasses (monocots), most are found in dicots. Tannins are low in young oak leaves but abundant in mature leaves (Feeny and Bostock 1968). Conversely, various secondary compounds are abundant in juvenile twigs of willows, birches, and white spruce in Alaska and Canada but sparse in mature twigs of 3 years and older (Bryant and Kuropat 1980). Thus the palatability and availability of food for herbivores differs between seasons and between years because of changes in the concentration of secondary compounds.

There are three major classes of secondary compound: terpenes; soluble phenol compounds; and alkaloids, cardenolides, and other compounds.

#### Terpenes

These are cyclic compounds of low molecular weight and usually one to three rings. They inhibit the activity of rumen bacteria (Schwartz *et al.* 1980) and are bitter tasting or volatile. Examples are essential oils from citrus fruits, carotene, eucalyptol from eucalyptus, papyriferic acid in paper birch, and camphor from white spruce. Camphor and papyriferic acid act as antifeedants to snowshoe hares (Bryant 1981; Sinclair *et al.* 1988), while  $\alpha$ -pinene from ponderosa pine deters tassel-eared squirrels (*Sciurus alberti*) (Farentinos *et al.* 1981).

#### Soluble phenol compounds

The main groups of these chemicals are the hydrolyzable and condensed tannins (McLeod 1974). They act by binding to proteins and thus make them indigestible. The name "tannin" comes from the action of polyphenols on animal skins, turning them into leather, which is not subject to attack by other organisms, in a process called "tanning."

Tannins are widespread among plant species, occurring in 87% of evergreen woody plants, 79% of deciduous woody species, 17% of annual herbs, and 14% of perennial herbs. Tannins have negative physiological effects on elk (Mould and Robbins 1982) and may determine food selection by browsing ungulates in southern Africa (Owen-Smith and Cooper 1987; Cooper *et al.* 1988) and snowshoe hares in North America (Sinclair and Smith 1984). Domestic goats (*Capra hircus*) learn to avoid young twigs of blackbrush (*Coleogyne ramosissima*) due to condensed tannins (Provenza *et al.* 1990).

2.3.3 Plant secondary compounds

#### Alkaloids, cardenolides, and other compounds

These are cyclic compounds with nitrogen atoms in the ring. They occur in 7% of flowering plants, and some 4000 compounds are known (Robbins 1983). Some alkaloids are nicotine, morphine, and atropine. They have several physiological effects, but act more as toxicants or poisons than as digestion inhibitors. Some alkaloids, such as cardenolides in milkweed (Asclepiadaceae), are sequestered by insects such as the monarch butterfly (*Danaus plexippus*), whose larvae feed on milkweed. These noxious cardenolides act as emetics to birds. Young, inexperienced blue jays (*Cyanocitta cristata*) eat these insects, then regurgitate them; after this, they avoid them (Brower 1984). Cyanogenic glycosides, which release HCN on hydrolysis in the stomach, are sequestered by *Heliconius* butterflies from their passionflower (*Passiflora* species) food plants. These insects are avoided by lizards, tanagers, and flycatchers (Brower 1984).

#### 2.4 Measurement of food supply

2.4.1 Direct measures

The amount of food available to animals may be measured directly. For carnivores, some form of food sampling can be used: insect traps for insectivores; counts of ungulates for large carnivores. For grazing ungulates, McNaughton (1976) clipped grass in exclosure plots to measure the available production for Thomson's gazelle on the Serengeti Plains. Winter food supply for snowshoe hares was estimated from the abundance of twigs with a diameter of 5 mm on its two most common food plants, gray willow (*Salix glauca*) and bog birch (*Betula glandulosa*) (Smith *et al.* 1988; Krebs *et al.* 2001a). Pease *et al.* (1979) used a different approach, feeding a known quantity of large branches to hares in pens and measuring the amount eaten from these. Using this measure as the edible fraction of the large branches, they then estimated the total available biomass of edible twigs from the density of large branches in the hares' habitat.

The most serious problem with direct measures is that they all depend on the assumption that we can measure food in the same way that the animals come across it. It is rare that this assumption is valid: insects that enter pitfall traps or are collected by sweepnets are not the same fraction as is seen by a shrew or bird; ungulate censuses do not indicate which animals are actually available to carnivores, for we can be sure that not all are catchable.

If the food supply is relatively uncomplicated, such as the short green sward that is grazed uniformly by African plains antelopes, then we can measure it in a way resembling the feeding of animals. With woody plants, however, we cannot do so, and in most cases our estimates are simply crude indices of food abundance. Our errors can both over- and underestimate the true availability of food: we may include material that an animal would not eat, so producing an overestimate; or we may overlook food items because animals are better at searching for their own food than we are, so producing an underestimate. We can never be sure on what side of the true value our index lies, unless we calibrate it with another method.

2.4.2 *Fecal protein and diet protein and diet protein A* second method, which has been applied so far only to herbivores, allows the animal to choose its own food and so avoids the problems discussed in the previous section. Diet protein, energy, or other nutrients can be estimated by observing what animals eat and then determining the chemical composition of that diet. These indirect estimates of intake are compared with an estimate of requirements either based upon direct physiological experiments or inferred from the literature. Examples come from reindeer on South Georgia Island (Leader-Williams 1988) and greater kudu (*Tragelaphus strepsiceros*) in South Africa (Owen-Smith and Cooper 1989). Energy intake for the jerboa Fig. 2.1 Seasonal changes in energy and body weight of the jerboa (*Allactaga elater*) in the cis-Caspian, Russia, during 1985. (a) Percentage energy of forage in the stomach. (b) Daily energy intake, and daily energy requirement. (c) Body weight. (After Abaturov and Magomedov 1988.)



(*Allactaga elater*) in north cis-Caspian, Russia (Fig. 2.1), dropped below requirements in mid-summer, and so body weight declined (Abaturov and Magomedov 1988). Similarly, energy measured from fecal collections showed that the energy intake of moose in Norway during winter dropped below requirements by 25–30% (Hjeljord *et al.* 1994). For greater kudu (Fig. 2.2), energy intake during winter was below requirements, but protein intake was sufficient. In contrast, the protein intake of African buffalo in tropical dry seasons was below requirements (Fig. 2.3).

These indirect measures of food intake can often be inaccurate because they are an amalgam of several different measurements. One way around this is to use a physiological index from the animal to indicate the quality of the food it has eaten. Nitrogen in the feces predicts nitrogen in the diet down to the minimum level of nitrogen balance. If nitrogen intake falls below this level, it is not reflected in the feces, because metabolic nitrogen (from microorganisms and gut cells) continues to be passed out irrespective of intake.

In tropical regions, this relationship has been found for cattle (Bredon *et al.* 1963), buffalo, and wildebeest (Sinclair 1977), and in North America, for cattle, big-horn sheep (*Ovis canadensis*), elk, and deer (Fig. 2.4) (Leslie and Starkey 1985; Howery and Pfister 1990). These relationships apply to ruminants eating natural food. Similar relationships have been found for experimental diets in Australian rabbits (Myers and

Fig. 2.2 Monthly changes in the estimated daily nutrient intakes of greater kudu relative to estimated maintenance requirements. (a) Crude protein intake (dashed line); available protein (solid line); protein requirement for metabolic turnover, fecal loss, and growth (dotted line). (b) Metabolizable energy intake (solid line); metabolizable energy requirement for resting, activity, and growth (dotted line). (c) Phosphorus intake (solid line); phosphorus requirement (dotted line). (After Owen-Smith and Cooper 1989.)



Bults 1977), snowshoe hares (Sinclair *et al.* 1982), elk, and sheep (Mould and Robbins 1981; Leslie and Starkey 1985), although the slopes of the regression lines differ from the natural diets.

A potential problem with this approach is that plant secondary compounds such as tannin may obscure the relationship by causing higher amounts of metabolic nitrogen to be passed out (Robbins *et al.* 1987; Wehausen 1995). This has been observed in experimental diets with high amounts of these compounds (Mould and Robbins 1981; Sinclair *et al.* 1982). However, these are abnormal situations and when animals are allowed to choose their own diet the relationship holds up. The regression has been determined for only a few species on natural diets, so more work is needed in this area.





Fig. 2.4 Correlation of dietary nitrogen with fecal nitrogen in (a) elk and (b) black-tailed deer. Nitrogen increases with season. Spring ( $\bigstar$ ); summer ( $\bullet$ ); fall ( $\Delta$ ); winter ( $\bigcirc$ ). (After Leslie and Starkey 1985.)

A second potential problem could arise if fecal samples were exposed to the weather and the nitrogen leached out. For white-tailed deer feces in autumn, the bias is minimal if samples are collected less than 24 days after defecation (Jenks *et al.* 1990).

The relationship between fecal nitrogen and dietary nitrogen can be used to estimate whether animals are obtaining enough food for maintenance. In African buffalo, the estimate of dietary nitrogen was compared with estimates of dietary nitrogen from rumen contents (Fig. 2.3). The two are similar.

A comparable approach has related fecal nitrogen directly to weight loss. Thus, Gates and Hudson (1981) found that elk lost weight below about 1.6% fecal nitrogen (Figure 2.5a) during late winter when there was deep snow (Fig. 2.5b).

#### 2.5 Basal metabolic rate and food requirement

2.5.1 Energy flow

The flow of energy through the body is illustrated in Fig. 2.6. Energy starts as consumption energy or intake energy. Part of this is digested in the gut and passes through the gut wall as digestible energy; the rest is passed out in the feces as fecal energy. Part of the digestible energy is lost in the urine and the remainder, called metabolic or assimilated energy, can then be used for work. The work energy can be divided into two further subtypes: respiration energy, which is used for the basic maintenance of



Fig. 2.5 (a) Body weight gain of male elk (•) and calves (O) in Alberta can be predicted from the percentage of fecal crude protein. (b) Seasonal changes in the percentage of fecal crude protein are related to snow depth. (After Gates and Hudson 1981.)

Fig. 2.6 Flow chart of

energy through the body.



the body (resting energy) and for activity, and production energy, which is used for growth and reproduction.

The flow chart for protein is similar, except that protein is normally used only for production. Protein is not used in respiration except under special conditions of food shortage, when it is broken down (catabolized) to provide energy.

Metabolic energy (*M*) can be measured in two ways:

1 In the laboratory, by measuring resting energy and activity to obtain the respiration component (R) and from growth and population studies to obtain production (P), so

that:

M = R + P

**2** In the field, by measuring consumption (*C*) and fecal (*F*) and urinary (*U*) outputs, so that:

M = C - F - U

2.5.2 Basal metabolic rate

Basal metabolism is the energy needed for basic body functions. The energy comes from oxidation of fats, proteins, and carbohydrates to produce water and  $CO_2$ . Thus, maintenance energy can be measured from expired air volume and composition because intake air has a stable composition of 20.94% oxygen, 0.03% carbon dioxide, and 79.03% nitrogen. Since 6 moles of  $CO_2$  and water are produced with 673 kcal of heat, the  $CO_2$  in expired air can be used to calculate the rate of energy used for maintenance. Measurements can be obtained either in chambers or from gas masks, and the animal must be in its thermoneutral zone (not shivering, panting, or sweating), resting, and not digesting food. Such conditions give the basal metabolic rate.

When plotted against log of body weight, the basal metabolic rates (BMRs) of different eutherian mammalian groups, such as those in Fig. 2.7, fall on a line whose slope is approximately 0.75. Thus, Kleiber (1947) produced the general equation:

$$BMR = 70 W^{0.75}$$

where BMR is in kcals per day and *W* is body weight in kilograms. This is an average over all mammals. Specific groups may differ: desert-adapted mammals have lower rates, marine mammals higher ones. Large nonpasserine birds are similar to eutherians, but the smaller passerines are 30–70% higher. The constant 70 also differs; in marsupials it is 48.6 and in the echidna (a monotreme) 19.3 (Robbins 1983). McNab (1988) predicted that animals feeding on lower-energy foods should lower their BMR. Experiments in Chile with the burrowing rodent (*Octodon degus*) fed on low- or high-fiber diets have confirmed this prediction (Veloso and Bozinovic 1993).



Fig. 2.7 Relationship of basal metabolic rate and body weight in different groups of small mammals. (After Clutton-Brock and Harvey 1983, which is after Mace 1979.) Hibernating mammals, such as ground squirrels, can lower their body temperatures to a few degrees above ambient temperature, but no lower than about 0°C. Hummingbirds can lower their body temperature to about 15°C, in a process called torpor. Both hibernation and torpor save energy (Kenagy 1989; Kenagy *et al.* 1989).

So far, we have discussed resting or maintenance requirements. Activity adds a further energy cost to maintenance. Standing is on average 9% more costly than lying for mammals and 13.6% for birds (Robbins 1983). The cost of locomotion is similar for bipedal and quadrupedal animals (Fedak and Seeherman 1979). Cost of locomotion (LC), expressed as kcal/kg/km, declines linearly with increasing log body size. Thus:

 $LC = 31.10 W^{-0.34}$ 

where W is in grams.

Hence, the cost of moving is higher per unit body mass for smaller species and juveniles.

Average daily metabolic rate (ADMR, the sum of resting and activity rates) is approximately  $2 \times BMR$  in captive mammals, but it is difficult to measure for free-living animals. For captive passerines, ADMR is  $1.31 \times BMR$ , and for captive nonpasserines,  $1.26 \times BMR$ . As a rough approximation, free-living birds and small mammals have a metabolic rate two to four times BMR.

2.5.3 *Variation in food requirements* The ADMR and other average measures of metabolic rate hide seasonal fluctuations *in food requirements* in food and energy demands. The costs of reproduction add considerably to those for normal daily activity. In the red deer and the wildebeest, the rut imposes a considerable energetic cost upon males, which spend several weeks fighting, defending territories, and herding females while eating very little (Sinclair 1977; Clutton-Brock *et al.* 1982). Males put on large amounts of body fat before the rut and use it to cover the extra energy requirements it imposes. Mule deer males (Fig. 2.8a) deposit kidney fat in autumn and use it during mating in November (Anderson *et al.* 1972).

Female mammals use additional energy for lactation and to grow a fetus. Like males, they accumulate body fat, especially in the mesentery and around the kidneys, before birth and lactation. During the last third of gestation, metabolic costs are twice ADMR, and during lactation they are three times ADMR. In female mule deer (Fig. 2.8b), fat is built up in autumn and early winter and used during gestation, birth, and lactation between late winter and summer. Thus, the timing of reproduction in ungulates is influenced in part by the need to obtain good food supplies and to build up fat reserves.

#### 2.6 Morphology of herbivore digestion

2.6.1 *Strategies of digestion* 

Carnivores and omnivores digest their food in the stomach and small intestine. The small intestine is relatively short in these species. Herbivores, which make up most (about 90%) of the mammals (Björnhag 1987), need to digest large amounts of fairly indigestible cellulose and hemicellulose, and have thus adapted the gut to increase retention time. One strategy is to evolve a much longer small intestine. An exception is the giant panda, which evolved from bears and has retained the short intestine. In this species, organic matter digestibility is only 18%, one of the lowest recorded (Schaller *et al.* 1985). Another adaptation is to use microorganisms (bacteria, fungi, protozoa), which digest cellulose through fermentation. Plant material must be retained in a fermentation chamber long enough for the microorganisms to cause fermentation. Squirrels eat high-energy foods such as seeds, fruits, and insects and so do not need such

Fig. 2.8 Seasonal changes in the kidney fat index of mule deer are closely associated with reproduction and season. (a) Males; (b) females. (After Anderson *et al.* 1972.)



mechanisms. Some species have unusually low metabolic rates and hence longer retention times. Most are arboreal folivores: koalas (*Phascolarctos cinereus*) (Dawson and Hulbert 1970), sloths, and hyraxes (Rubsamen *et al.* 1979; Björnhag 1987). Reviews of digestive adaptations can be found in Hume and Warner (1980), Hornicke and Björnhag (1980), Robbins (1983), Björnhag (1987), and Chivers and Langer (1994).

2.6.2 *Ruminants* True ruminants, which include the bovids (cattle, sheep, antelopes), cervids (deer), tylopodids (camels), and giraffes, have an extension of the stomach divided into three chambers. One of these is the rumen, which acts as the fermentation chamber. Plant food is gathered without chewing and stored in the chamber during a feeding period. This is followed by a rumination period, during which portions of compacted food (bolus) are returned to the mouth for intensive chewing. In this way, coarse plant material is broken down mechanically and made available to the microorganisms for fermentation. The amount of fiber in the food determines how coarse it is; the coarser the food, the longer the process of grinding and fermentation. There is a limit to how

coarse the food can be before fermentation takes so long that the animal uses more energy than it gains. On average, a ruminant retains food in the gut for about 100 hours.

Microorganisms break down cellulose into short-chain fatty acids and proteins into amino acids and ammonia, which they use to produce more microorganisms. The host animal obtains its nutrients by digesting the dead microorganisms in the stomach and short intestine. The system is efficient, and digestibilities of organic matter and protein are around 65–75% are achieved for medium- to good-quality food (i.e. relatively low in fiber). Another advantage is that nitrogen can be recycled as urea. A disadvantage is that microorganisms digest nutrients that could be used directly by the host, which leads to a loss of energy through production of methane. Another is that ruminants cannot digest very high-fiber diets.

2.6.3 *Hindgut* In contrast to the foregut fermenters, or ruminants, a number of animal groups have developed an enlarged colon or caecum, or both, for fermentation. Large animals (over 50 kg) are in general colon fermenters, while small ones (under 5 kg) that feed on fibrous food are caecum fermenters.

#### **Colon fermenters**

In most cases, both the colon and the caecum are enlarged to hold fiber for microbial digestion. There is little separation of material into small particles and microbes on the one hand and fiber on the other, and there is little evidence that microbial proteins are digested and absorbed, although fatty acids can be absorbed.

Animals in this group are perissodactyls (horses, rhinos, tapirs), macropods (kangaroos), and perhaps elephants, wombats (*Vombatus ursinus*), and dugongs (*Dugong dugon*). These are all large animals and so do not need to ingest large amounts of energy and protein per unit of body weight (see Section 2.5.2). Since food material can be retained in the gut for longer periods in large animals, the rate of passage may be slow enough to allow fermentation and absorption of fatty acids to take place. None of these animals eat their feces, a practice called *coprophagy*.

#### Caecum fermenters

Small animals (less than 5 kg) have a relatively high metabolic rate. Those species which consume high-fiber diets such as grasses and leaves need to use the microbial protein produced by hindgut fermentation. They do so by coprophagy. In conjunction with this process, there is a sorting mechanism in the colon that separates fluids, small particles of food, and microbes from the fiber. The fluids and microbes are returned by antiperistaltic movements to an enlarged caecum for further fermentation and digestion. This mechanism therefore retains the nutrients long enough for fermentation. It is necessary because small animals cannot hold food material long enough to allow fermentation under normal passage rates.

Dead microbial material is passed out in the form of special soft pellets, *caecotrophs*, and these high-nutrient feces are eaten directly from the anus, a behavior called *caecotrophy*. The sorted high fiber is passed out as hard pellets, which are not re-ingested.

Animals that both ferment food in the caecum and practice caecotrophy include myomorph rodents (voles, lemmings, brown rat), lagomorphs (hares, rabbits), some South American rodents (coypu, guinea pig, chinchilla), and some Australian marsupials, such as the ringtail possum (*Pseudocheirus peregrinus*) (Chilcott and Hume 1985).

Two marsupials, the koala and the greater glider (*Petauroides volans*), feed on arboreal leaves and have caecal fermentation and a colonic sorting mechanism (Cork and Warner 1983; Foley and Hume 1987). Neither practice caecotrophy. At least in the koala, both the metabolic rate and the passage time are slow enough that caecotrophy is not necessary.

Björnhag (1987) identifies four strategies employed by small mammals that feed on plants:

1 Eat only highly nutritious plant parts, such as seeds, berries, birds, and young leaves. Squirrels fall into this group.

2 Have a low metabolic rate for your size so that fermentation is prolonged. Koala and tree sloths are examples of this group.

3 Separate digesta in the colon and retain easily digestible food particles plus microorganisms so as to allow fermentation of fibrous material being sorted and passed out.

4 Separate and retain only the microorganisms so as to allow rapid fermentation. Both 3 and 4 recirculate protein-rich fecal material by re-ingestion through caecotrophy. Examples are voles, lemmings, and lagomorphs. Foley and Cork (1992) review these strategies of digestion and their limits.

#### 2.7 Food passage rate and food requirement

The passage rate of food through an animal depends on the *retention time*, which is the mean time an indigestible marker takes to pass through. Various markers can be used, including dyes, glass beads, radioisotopes, and polyethylene glycol. Certain rare earth elements (samarium, cerium, and lanthanum) bind to plant fiber and provide useful markers by which to measure fiber passage times (Robbins 1983).

The rate of food intake by herbivores depends on the nutritive quality of the food. For example, in domestic sheep (Fig. 2.9) and white-tailed and mule deer, intake rate first increases and then decreases as the energy quality of food declines (Sibly 1981; Robbins 1983). This relationship occurs because both energy and protein are inversely related to fiber content.

Estimation of fecal protein can be used as a means of determining whether a population is obtaining enough food, because protein intake is related to the amount of protein in the feces (see Fig. 2.4). This method has been used to predict the change in body weight of elk (see Fig. 2.5b) (Gates and Hudson 1981) and to monitor food requirements in snowshoe hares (Sinclair *et al.* 1988).

Fig. 2.9 Relationship of intake rate to energy content of food in domestic sheep. Below an energy content of 590 J/g, intake rate falls because of a finite gut capacity and declining fermentation rates. Rate of intake is dry matter/day/body weight<sup>0.75</sup>. (After Sibly 1981, which is after Dinius and Baumgardt 1970.)



### 2.8 Body size and diet selection

The gut (i.e. the rumen, large intestine, and caecum, as well as the crops of hummingbirds and the cheek pouches of heteromyid rodents) has a capacity that is a linear function of body weight ( $W^{1.0}$ ) (Clutton-Brock and Harvey 1983; Robbins 1983). Energy requirements, however, are a function of metabolic body weight ( $W^{0.75}$ ). Thus, the difference between the exponents ( $W^{1.0}/W^{0.75} = W^{0.25}$ ) means that a larger animal can eat more food relative to requirement than a smaller animal. This can be expressed in two ways: (i) on the same quality of diet, a larger animal needs to eat less food per unit of body weight than does a smaller one; and (ii) a larger animal on a lower-nutrient diet can extract the same amount of nutrient per unit of body weight as a smaller animal on a higher-nutrient diet. Thus, larger animals can eat higher-fiber diets, a feature that allows resource partitioning in African ungulates (Bell 1971; Jarman and Sinclair 1979).

Jarman (1974) extended the relationship between body size and diet in African ungulates to explain interspecific patterns of social and anti-predator behavior. We can identify five categories, from selective browsers to unselective grazers:

1 Small species (3–20 kg), solitary or in pairs, which are highly selective feeders on flowers, birds, fruits, seed pods, and young shoots. Their habitats are thickets and forest, which provide cover from predators. There is little sexual dimorphism and both sexes help in defending a territory. This group includes duikers (*Cephalophus* species), suni antelope (*Nesotragus moschatus*), steinbuck (*Raphicerus campestris*), dikdik (*Madoqua* species), and klipspringer (*Oreotragus oreotragus*).

**2** Small to medium species (20–100 kg), which can be both grazers and browsers, but are very selective of plant parts, as in **1**. Their habitat is riverine forest, thicket, or dense woodland. Group size is larger, from two to six, comprising one male and several females. There is some sexual dimorphism. Predators are avoided by hiding and freezing. They are usually territorial and include lesser kudu (*Tragelaphus imberbis*), bushbuck (*T.scriptus*), gerenuk (*Litocranius walleri*), reedbuck (*Redunca* species), and oribi (*Ourebia ourebia*).

**3** Medium-size species (50–150 kg), which are mixed feeders, changing from grazing in the rains to browsing in the dry season. Habitats are varied and range from dense woodland and savanna to open flood plains. There is one male per territory. Female group size is variable (6–200). Females do not defend a territory, but wander through the male territories. Nonterritorial male groups are excluded from territories and behave like female groups. Females have a large home range, which is smaller in the dry season than in the wet season. This group is sexually dimorphic in the extreme. Predators are avoided by group vigilance and by running. Species typical of this group include impala, greater kudu, sable, kob (*Kobus* species), lechwe, and gazelles (*Gazella* species).

4 Medium to large species (100–250 kg), which are grazers, selecting high-quality grass leaves. Males are single and territorial or form large bachelor groups. Female groups range from six to many hundred. They have a large home range, often divided into wet- and dry-season ranges separated by a considerable distance. Habitats are generally open savanna and treeless plains. Predators are avoided by group vigilance and running. Sexual dimorphism is present but less extreme than in 3. This group includes wildebeest, hartebeest, topi (*Damaliscus korrigum*), and Grevy's zebra.

5 Large species (> 200 kg), which are unselective grazers and browsers of low-quality food. Habitats are closed woodland and open savanna. Movements are seasonal.

Males are nonterritorial and form a dominance hierarchy. Females form groups of ten to several hundred and have a large home range. Active group defense against predators is shown by African buffalo and African elephant, while other species use group vigilance and running to avoid predation. This group includes Burchell's zebra (*Equus burchelli*), giraffe (*Giraffa camelopardalis*), eland (*Taurotragus oryx*), gemsbok (*Oryx gazella*), and Roan antelope (*Hippotragus niger*).

Jarman's (1974) categories relate body size inversely to food supply, because low-quality food is more abundant. This allows species to form larger groups in order to avoid predators, and the size of group then determines how a male obtains his mate. In small species, males keep females in their territories year-round, and this may be the only way of finding females in estrus. When female groups are larger (group **3**), females cannot remain within one territory. Males thus compete for territories within the females' home range, providing an opportunity for mating as females move through the territory. These territories are for mating and not to provide year-round food.

Finally, interspecific competition for male mating territories may have led to larger males with elaborate weapons. Since these selection pressures have not operated on the females, which have remained at a smaller size, sexual dimorphism develops. Thus, we see a connection between body size, food quality, group size, predator defense, and mating system.

In other groups of animals, gut size can be phenotypically plastic, varying with food availability and season, particularly in birds (Piersma and Lindstrom 1997). Thus, garden warblers (*Sylvia borin*) migrating over the Sahara reduce their gut size and hence food intake (McWilliams *et al.* 1997).

## 2.9 Indices of body condition

2.9.1 *Body weight and total body fat* 

Body weight and fat reserves affect survival and reproduction in mammals (Hanks 1981; Dark *et al.* 1986; Gerhart *et al.* 1996) and birds (Johnson *et al.* 1985). Body weight can be measured directly for small mammals such as the jerboa (Fig. 2.1) and for birds. Weight changes seasonally in response to changes in food supply and hence intake.

Body weight is a function of genetic determinants, age, and the amount of fat and protein stored in the body. In order to monitor fat and protein changes, it is better to remove the effects of body size (the genetic and age components). This can be done by using a ratio of weight to some body measure that is a function of size. Thus, for cottontail rabbits (*Sylvilagus floridanus*), Bailey (1968) found a relationship between predicted body weight (PBW, in g) and total length (L, in cm) such that:

 $PBW = 16 + 5.48 (L^3).$ 

The condition index for the rabbits would then be the ratio of observed weight to predicted weight. A similar relationship has been found between foot length and weight for snowshoe hares (O'Donoghue 1991). Murray (2002) found that the bone-marrow fat of snowshoe hares was predicted by the ratio of body weight to foot length. Kruuk *et al.* (1987) used a general equation for European otters (*Lutra lutra*) in which the index of body condition (K) was related to mean body weight (W, in kg) and body length (L, in m) by:

 $K = W/(aL^n)$ 

where a = 5.02 and n = 2.33.

At the other extreme of size, blubber volumes of fin whales (*Balaenoptera physalus*) and sei whales (*B.borealis*) have been calculated from body length, girth, and blubber thickness measured at six points along the carcass (Lockyer 1987).

Although body weight alone is a satisfactory measure of condition for such birds as sandhill cranes (*Grus canadensis*) and white-fronted geese (*Anser albifrons*) (Johnson *et al.* 1985), it is usually better to account for body size using some measure such as wing length, tarsus length, bill length, or keel length.

In female mallards (*Anas platyrhynchos*), fat weight (F), an index of condition, is related to body weight (BW) and wing length (WL) by:

F = (0.571 BW) - (1.695 WL) + 59.0

A similar relationship holds for males (Ringelman and Szymczak 1985).

In maned ducks (*Chenonetta jubata*) in Australia, female body weight and total fat increase before laying. Some 70% of the fat is used during laying and incubation. Protein levels, however, do not change (Briggs 1991). Among northern-hemisphere ducks, there are four general strategies for storing nutrients prior to laying:

1 Fat is deposited before migration and is supplemented by local foods on the breeding grounds, as demonstrated by mallard.

**2** Reserves are formed entirely before migrating to the breeding area, as in lesser snow geese (*Chen caerulescens*).

3 Reserves are built up entirely on the breeding grounds with no further supplementation, as illustrated by the common eider (*Somateria mollissima*).

4 Body reserves are both formed in the breeding area and supplemented by local food, as seen in the wood duck (*Aix sponsa*) (Owen and Reinecke 1979; Thomas 1988).

Both ducks and game birds can alter the lengths of their digestive systems in response to changes in food supply. Under conditions of more fibrous diets during winter, gut lengths increased in three species of ptarmigan (Moss 1974), gadwall (*Anas strepera*), and mallard (Paulus 1982; Whyte and Bolen 1985).

In passerine birds, energy is stored in various subcutaneous and mesenteric fat deposits, and protein is stored in flight muscles. The latter varies with total body fat, as in the yellow-vented bulbul (*Pycnonotus goiavier*) in Singapore (Ward 1969) and the house sparrow (*Passer domesticus*) in England (Jones 1980). In the gray-backed camaroptera (*Camaroptera brevicaudata*), a tropical African warbler, both total body fat and flight-muscle protein vary in relation to laying date (Fig. 2.10) (Fogden and Fogden 1979).

As in body-weight measures, flight-muscle weights are corrected for body size by dividing by a standard muscle volume (SMV). Davidson and Evans (1988) used the formula:

 $SMV = H(L \times W + 0.433 C^2)$ 

for shorebirds of the genus *Calidris*, where H is the height of the keel of the sternum, L is the length of the keel of the sternum, W is the width of the raft of the sternum (one side only), and C is the distance from the keel to the end of the coracoid.

Direct measures of body weight are feasible with birds and small mammals but impractical for large mammals, for which some other index of body condition and food reserves must be used. These have been reviewed by Hanks (1981) and Torbit *et al.* (1988). Large mammals store fat subcutaneously, in the gut mesentery, around

Fig. 2.10 Total body fat (●) and flight muscle index (○) are related to laying day in the female gray-backed camaroptera (a tropical African warbler). Eggs are laid on days 1–3. Flight muscle index is the ratio of (lean dry flight muscle weight)/(flight muscle cord<sup>3</sup>). The broken line indicates estimates. (After Fogden and Fogden 1979.)

2.9.2

index



the kidneys and heart, and in the marrow of long bones. The fat stores are used up in that order (Mech and DelGiudice 1985). Because of this sequential use, no single fat deposit is a perfect indicator of total body fat. In caribou, for example, a combination of body mass and a visual index of condition provided the best predictor of fatness (Gerhart *et al.* 1996). Particular fat stores are of interest for specific purposes, such as reproduction (kidney fat) or starvation (bone marrow fat). For these purposes, they provide a reasonable guide for managers, and total body fat is less useful.

*Kidney fat* Ungulates accumulate fat around the kidney and in other places in the body cavity in anticipation of the demands of reproduction. We saw in Section 2.5.3 how the fat reserves of mule deer change according to the stage of the reproductive cycle (Fig. 2.8), the timing of these changes differing between the sexes.

Although there is little relationship between kidney fat and total body fat in some species (Robbins 1983), others, such as most African ruminants, show a close relationship (Smith 1970; Hanks 1981). For white-tailed deer, the percentage of fat in the body is related to the kidney fat index (KFI) by (Finger *et al.* 1981):

% fat = 6.24 + 0.30 KFI

In mule deer, both the weight of kidney fat and the KFI are correlated with total body fat (Anderson *et al.* 1969, 1972, 1990; Torbit *et al.* 1988).

Although a similar relationship was found for the brush-tailed possum (*Trichosurus vulpecula*) in the South Island of New Zealand (Bamford 1970), a better correlation was found between total body fat and mesenteric fat.

KFI has been measured in two ways:

1 The kidney is pulled away from the body wall by hand and the surrounding connective tissue and embedded fat tears away along a natural line posterior to the kidney. A cut along the mid-line of the kidney allows the connective tissue to be peeled away cleanly. The KFI is the ratio of connective tissue plus fat weight to kidney weight summed for both kidneys.

2 The connective tissue is cut immediately anterior and posterior to the kidney, so that only the fat immediately surrounding the kidney is used. This has the small advantage of being more objective than 1, but the much greater disadvantage of discarding most of the tissue where fat is deposited, so that much of the relevant variability in fat deposition is lost. Hence, the first method may be the more useful index. Fig. 2.11 Kidney fat index (the ratio of kidney-plus-fat weight to kidney weight) is depleted almost entirely before bone marrow fat declines in ruminants. (After Hanks 1981.)



2.9.3 Bone marrow fat

Bone marrow fat does not decline until after most of the kidney fat has been used (Fig. 2.11) in temperate and tropical ungulates and in some marsupials (Ransom 1965; Bamford 1970; Hanks 1981). In mule deer, marrow fat changed most rapidly at very low levels of total body fat (Torbit *et al.* 1988). Consequently, a decline in bone marrow fat reflects a relatively severe depletion of energy reserves and therefore provides an index of severe nutritional stress, as was found for starving proghorn antelope (Depperschmidt *et al.* 1987).

Mobilized marrow fat is replaced by water. Hence, the ratio of dry weight to wet weight of marrow is a good measure of fat content. A number of studies on both temperate and tropical ruminants (Hanks 1981) indicate as a close approximation that:

% marrow fat = % dry weight -7.

Dry weight of marrow is measured from the middle length of the marrow in one of the long bones, avoiding the hemopoitic ends. The method has been used on wildebeest (Fig. 2.12) and deer (Klein and Olson 1960) to establish whether they had died from lack of food.

Broad categories of marrow fat content in ruminants are provided by the color and texture of the marrow (Cheatum 1949). This method is quick (it avoids collection

Fig. 2.12 Marrow fat of wildebeest (broken line) dying from natural causes in Serengeti is related to season and the percentage of crude protein in their diet (solid line, with 95% confidence limits). (After Sinclair 1977.)



of marrow) and is sufficient to determine whether an animal has been suffering from undernutrition at death (Verme and Holland 1973; Kirkpatrick 1980; Sinclair and Arcese 1995). The categories with approximate fat values are:

1 *Solid, white, and waxy* The marrow can stand on its own and contains 85–98% fat. Such animals are not suffering from undernutrition.

2 White or pink, opaque, gelatinous The marrow cannot stand on its own and covers a broad range of fat values (15–85%). Such animals have depleted fat reserves.
3 Yellow, translucent, gelatinous The clear, gelatinous appearance is distinctive, and indicates there is less than 15% fat, and often only 1%. Such animals are starving.

2.9.4 *Bioelectrical* Bioelectrical impedance analysis uses an electrical current passed through anaesthetized animals in a bioelectrical impedance plethysmograph. Resistance (R) and reactance  $(X_c)$  of the current are recorded and are related to impedance (Z) by:

 $Z = \sqrt{(R^2 + X_c^2)}$ 

In wombats (*Lasiorhinus latifrons*), resistance is a good predictor of total body fat (Woolnough *et al.* 1997). The technique has also been applied to seals (Gales *et al.* 1994) and bears (Farley and Robbins 1994).

2.9.5 *Blood* and urine indices of condition Blood parameters as indices of condition and food intake are potentially useful for living animals that are too large to be easily weighed. However, blood characteristics are not well known for most species. More work is needed. Different parameters have been examined in different studies. Plasma non-esterified fatty acid, protein-bound iodine, and serum total protein were all related to nutrition in Australian tropical cattle (O'Kelly 1973). Body condition of moose has been related to various sets of blood parameters, ranked according to their sensitivity (Franzmann and LeResche 1978). Starting with the single best parameter, sensitivity increased with the addition of other measures: (i) packed cell volume (PCV), (ii) PCV plus hemoglobin content (Hb), (iii) PCV, Hb, Ca, P, and total blood protein (TP), and (iv) PCV, Hb, Ca, P, TP, glucose, albumin, and  $\beta$ -globulin.

Protein loss from the body was strongly correlated with body weight loss in white-tailed deer on experimentally restricted diets. Serum urea nitrogen and the ratio of urinary urea nitrogen to creatinine were the best blood and urine indicators of undernutrition and protein loss (DelGiudice and Seal 1988; DelGiudice *et al.* 1990). For example, serum urea nitrogen is a good indicator of recent protein intake in white-tailed deer (Brown *et al.* 1995). Similarly, the ratio of urinary urea nitrogen to creatinine provided a reasonable predictor of physiological responses to nutrition in this species (DelGiudice *et al.* 1996)

2.9.6 *Problems* We have already noted that it is generally impractical to obtain measures of total body *with condition indices* fat in large mammals. Various single indices such as kidney fat and bone marrow fat have been used, but these are useful for specific purposes and cannot be used over the whole range of total body fat values. Kidney fat is more appropriate for estimating the upper range of body fat values, while bone marrow fat represents the lower values. A combination of six indices of body fat deposits in carcasses has been proposed (Kistner *et al.* 1980). This method is useful for complete carcasses but cannot be used for

animals dying naturally because the soft parts are usually eaten by predators and scavengers, or else they decompose. Under these conditions, the only index that remains uniformly useful is bone marrow fat.

Bone marrow fat as an index is biased towards the low-body-fat values. It cannot reflect changes in the higher levels of body fat, so very fatty bone marrow does not necessarily mean an animal is in good condition (Mech and DelGiudice 1985).

Many studies use some form of visual index of condition. However, studies in which total body fat has been measured directly find poor correlations with body condition indices (Woolnough *et al.* 1997).

Although blood indices may be useful as a means of assessing condition and nutrition in living animals, they require careful calibration. Many of the blood characteristics are influenced by season, reproductive state, age, sex, and hormone levels. More importantly, they can be altered rapidly by the stress of capture and handling. All of these factors could act to obscure and confound changes in nutrition.

All estimates of body condition taken from a sample of the live population are poor indicators of the nutritional state of the population for two reasons. First, such samples are biased towards healthy animals, because those in very poor condition are either dead or dying and not available for sampling. Second, the age groups that are most sensitive to density-dependent restriction in food supply – the very young and very old – form a small proportion of the live population. Thus, even a strictly random sample of the population will include a majority of healthy animals and consequently the mean value of condition will be very insensitive to changes in food supply. Therefore, it is unlikely that one can assess whether a population is regulated by food supply or by predators based solely on body condition samples of the live population. To make this assessment, one should look at the conditions of the animals that have died.

Summary Nutrition and feeding behavior underlie many critical issues in wildlife ecology and 2.10 management, such as the adequacy of food supplies for endangered species and the potential yield in response to harvesting. For carnivores, the nutrient composition of prey is usually well balanced to their specific needs, whereas in herbivores the foods eaten may be deficient in key nutrients, such as protein or sodium. Many plant tissues defend themselves against herbivory using poisons, protective structures such as spines, or chemicals that bind to ingested proteins, making them unavailable for digestion. In herbivores, it can also prove difficult to assess food availability in a meaningful way, because the plant tissues eaten represent only a small fraction of the plant biomass present. Various animal-based measures, such as fecal nutrient composition, have been developed to assess food availability and body condition from the herbivore's point of view. Nutritional constraints often vary disproportionately with body size. Many aspects of the behavior and ecology of wildlife species are closely tied to seasonal and spatial variation in food availability, including social organization, spacing patterns, breeding synchrony, and mating system.