

# CHAPTER 1

## INTRODUCTION

From an energetics viewpoint, mammals occupy a continuum which ranges from species having maximal energy intakes (energy ‘maximisers’) to species having minimal energy expenditures (energy ‘minimisers’). Energy ‘maximisers’ have metabolic rates higher than expected for their body size. These species have characteristics of high rates of energy intake (in terms of food) and high rates of growth, reproduction and activity. Energy ‘minimisers’ have metabolic rates lower than expected for their body size and can exhibit extreme energy conservatism; they have low rates of energy intake combined with physiological and behavioural adaptations to minimise daily energy expenditure, which include low rates of growth and reproduction, and energy-conserving activity strategies.

The three extant species of wombats (Marsupialia: Vombatidae) are large, terrestrial grazers that exhibit physiological and behavioural characteristics indicative of the energy conservative extreme of this energetics continuum. They have a low basal metabolic rate (Wells 1973) for their size, are able to utilise poor quality food (Wells 1973; Gaughwin *et al.* 1984; Barbosa *et al.* 1993), spend most of their time in deep burrows (Wells 1978; McIlroy 1995; Johnson 1991b), have low daily activity (Johnson 1991a), and have a large body size and compact body form. Wombats also have adaptations that set them apart from other mammalian herbivores; their digestive system and continuously growing teeth are both unique amongst Australian marsupials, and they have the distinction of being the world’s largest burrowing herbivore. Despite such

glimpses of what may be a collection of adaptations that are unique amongst mammals, there have been few detailed studies on wombats and consequently little physiological or ecological information exists beyond the natural history level. Energetics studies of wombats have been limited to their basal metabolism under laboratory conditions; little is known of the ecological energetics of free-living wombats.

Extreme energy conservatism undoubtedly plays a large part in enabling the three extant species of wombat to exist in habitats which are climatically harsh, such as semi-arid and sub-alpine (although they are not confined to these areas), and to utilise food resources which are of poor quality and often dry. The two semi-arid wombat species are also able to exist in habitats where rainfall and free water may not be present for weeks or even months. The aim of this study is to examine and quantify aspects of the energy-conserving adaptations in free-living wombats. Current information suggesting the existence of extreme energy conservatism in wombats is summarised later in this chapter (and details are given in subsequent chapters), together with an hypothesised 'adaptive syndrome' and the specific aims and hypotheses of this study. The following section gives theoretical background on the evolutionary responses of mammalian herbivores to energy constraints in food resources, the purpose of which is to provide a context within which to view the adaptive syndrome in wombats, and to provide a foundation for concepts discussed in subsequent chapters.

### ***Energetics: the link between metabolic rate, body size and diet.***

Energy intake and energy expenditure are fundamental in shaping and reflecting almost all aspects of the physiology, ecology and behaviour of an animal. Relationships between metabolic rate, body size and diet amongst herbivores have been recognised by numerous workers (eg. Bell 1970; Jarman 1974; Janis 1976; Demment and Van Soest 1985; Harvey *et al.* 1991; Owen-Smith 1992; Illius and Gordon 1992). Perhaps the most fundamental of these relationships is between metabolic rate and body size. Basal (resting) metabolic rate (BMR) varies with body size, according to the power function  $BMR = 70 W^{0.75}$ , where BMR is kcal/day and W is body mass in kg (Kleiber 1975). This 'average' relationship has been derived from a wide range of species and body sizes, though intraspecific regressions often yield exponents different from 0.75 (Thonney *et al.*

1976). The significance of this relationship is that larger animals require a greater *absolute* energy intake than smaller animals, but their energy requirement *per unit body mass* is less than that of smaller animals. In other words, smaller animals ‘burn up’ energy faster than larger animals. A commonly expounded reason for this empirical relationship is that smaller animals lose energy as heat at a faster rate than larger animals due to their greater surface area to volume ratio. However, surface area relationships explain only part of the scaling of metabolic rate, since surface area scales to an exponent of approximately two-thirds. Other area / body mass related processes may also be involved, such as ratio of body mass to skeletal mass and area of respiratory and absorptive surfaces.

Given that mass-specific metabolism increases as size decreases, smaller animals must maintain higher energy intakes relative to their body size than larger animals in order to maintain energy balance, or they must reduce energy expenditure by ‘switching off’ (torpor or hibernation). To maintain higher relative energy intakes, small mammalian herbivores are faced with either eating more food (per gram of body mass) or eating food higher in energy concentration, or some combination of both. Gut capacity largely determines the capacity for digestion in a mammalian herbivore by limiting both the quantity of food retained for digestion and throughput over time (Demment and Van Soest 1985; Foley and Cork 1992). Because gut capacity scales approximately isometrically with body size (Parra 1978; Demment and Van Soest 1985) smaller herbivores are constrained in their ability to increase their relative rate of food intake. Digestibility can also be depressed with high food intakes (Raymond *et al.* 1959; Tyrrell and Moe 1975; Batzli 1981). Small herbivores must therefore meet their ‘extra’ energy demand by maximising the energy (and nutritional) concentration of their food. Moreover, plants contain dietary fibre (cell wall constituents) which requires long fermentation times in the mammalian gut before energy can be extracted. Because of the small gut volumes and short digesta retention times, the energy in dietary fibre is generally not available to smaller herbivores. Without eating high quality food (high in energy and nutrients and low in fibre), small herbivores could conceivably ‘starve on a full stomach’. Larger animals have a longer gut length and hence longer absolute digesta retention times, and so are better able to extract energy from diets higher in fibre.

Plants are not an homogenous food resource. The energy content and digestibility of plant material varies widely between plant taxa, plant parts and plant age (Darlington and Hershberger 1968; Van Soest 1982; Demment and Van Soest 1985; Foley and Hume 1987). The digestibility of different plant components largely reflects their functionality and location within the plant; structural components (cell walls) contain cellulose, hemicellulose and lignin which are not easily digested, whereas the metabolic components (cell contents) contain sugars, proteins and storage carbohydrates, all of which are easily digested once the cell is ruptured. Plant reproductive parts tend to be higher in energy and lower in fibre (cell wall components) than leaves or stems. Younger plant parts and shorter lived plants have less structural components (fibre) and so tend to be more digestible. Grasses are generally a more digestible food resource than leaves of woody dicots, but require longer digestion times (Owen-Smith 1988). Digestibility of plant parts can vary amongst taxa. For example, leaves of tropical (C<sub>4</sub>) grasses have higher cell wall and lignin concentrations (and lower digestibility) than temperate (C<sub>3</sub>) grasses (Minson and McLeod 1970).

Plant parts which are high in energy and low in fibre form a small and usually dispersed proportion of the overall plant biomass available to herbivores (Jarman 1974). Therefore, small herbivores, must feed selectively in order to acquire food items with high concentrations of energy and nutrients ('concentrate selectors'). Large herbivores, with their correspondingly large absolute energy requirements, may not be able to maintain an adequate energy intake using this strategy because of the time and energy costs involved in locating and handling small, rare food items. Larger mammalian herbivores appear to adopt the strategy of maximising their energy intake by mostly utilising the relatively more abundant food resources that are more diluted in energy and nutrients ('bulk and roughage feeders') (Bell 1971; Jarman 1974; Sinclair 1977; Jarman and Sinclair 1979; Owen-Smith 1988).

### ***Digestive strategies***

The evolutionary response of mammalian herbivores to the quality and dispersion of food resources, influenced by the relationship between metabolic rate and body size, has produced several digestive strategies. The greatest difference between the digestive

strategies of mammalian herbivores occurs between the 'foregut' and 'hindgut' fermenters. Mammals do not possess the necessary enzymes to break down cellulose and instead rely on microbial fermentation in the digestive tract to extract energy from plant cell walls, and possibly to rupture cells. In foregut fermenters, the main site of microbial digestion is anterior to the region of intensive auto-enzymatic digestion and absorption (small intestine) whereas in hindgut fermenters it is posterior to this region. Two strategies have developed amongst foregut fermenters: the ruminant system (which includes all 'ruminants' such as cattle, deer and antelope) and the tubiform or sacciform forestomach system. Hindgut fermentation has also evolved two strategies: fermentation in the enlarged blind sac of the caecum or fermentation in the large intestine itself, the colon. In caecum fermenters, there is usually little microbial activity in the colon, whereas colon fermenters may also use the caecum (if present) as an extension of the colon fermentation region.

The location of the fermentation site along the gut determines how cell wall constituents (fibre) and cell contents are digested and how the products of digestion are absorbed. In both foregut and hindgut systems, gut microbes in the fermentation site break down the structural (cell wall) carbohydrates. Much of the energy (and some nutrients) released during this process are not directly available to the host herbivore because they are rapidly absorbed by the gut microbes. The major energy source for the herbivore from fermentation is the waste products of microbial respiration (mainly volatile fatty acids) which are absorbed directly by the host. Foregut fermenters are able to recover nutrients (such as B-vitamins and amino acids, most of which have been synthesised by microbes) together with some energy, by digestion of the microbial bodies further down the gut. Hindgut fermenters are able to recover some of the nutrients from fermentation (such as short-chain fatty acids and some B-vitamins) across the colon, but other synthesised microbial nutrients (such as intact amino acids) are largely lost to hindgut fermenters. Some hind-gut fermenting species (mostly rodents and lagomorphs) have developed coprophagy to help counteract high faecal nutrient loss (McBee 1977; Kinnear *et al.* 1979). In the ruminant system, the foregut is modified to delay selectively the high fibre components of the diet for longer fermentation (Langer 1988). Fibrous components remain in the rumen and reticulum until remastication and fermentation have

reduced particle size. Colon fermenters also tend to retain larger particles in the gut longer than smaller particles and fluid. Conversely, caecal fermenters retain fluid and fine particles selectively in the caecum and excrete the large, relatively indigestible, fibrous particles more quickly (Hume 1989). As well as fermenting the structural carbohydrates, microbes in the foregut also ferment the easily digestible soluble (cell contents) carbohydrates. Fermentation of soluble carbohydrates releases less energy to the host than gastric (auto-enzymatic) digestion because of the extra trophic level between the herbivore and its food supply (Janis 1976; Demment and Van Soest 1985). Energy lost from methane production during fermentation can reduce energy assimilated by the herbivore by 20% (Black 1971). Hindgut fermenters avoid this energy loss by digesting the soluble carbohydrates in the gastric system (small intestine) before they pass into the fermentation chamber. Van Soest (1982) considers hindgut fermenters to be 'cell content specialists' whereas ruminants are 'cell wall specialists'.

### ***Digestive Strategy, Body Size and Feeding Ecology***

Digestive strategy is influenced by body size. In a world context, ruminants (artiodactyl ungulates) now dominate the middle size range for herbivores, but are absent in very small or very large sizes (Bell 1971; Jarman 1974; Demment and Van Soest 1985; Langer 1988). Non-ruminant foregut fermenters (such as camels, peccaries, hippopotamus, macropodids, sloths and some primates) and hindgut fermenters are found in all sizes, though hindgut fermenters dominate in the small and large size extremes. Amongst hindgut fermenters, colon fermenters are mainly large or very large herbivores such as dugongs, manatees, elephants and the perissodactyl ungulates (horses, zebra, tapirs and rhinos) whereas caecal fermenters are mostly small herbivores such as lagomorphs, rodents, hyraxes and phalangerids. Although the ruminant strategy did not evolve amongst Australia's herbivores, the relationship between body size and the use of foregut and hindgut strategies is similar to that observed on other continents. Foregut fermentation dominates medium and large sized herbivores (no extant Australian herbivores are very large) whereas hindgut fermentation dominates amongst small sizes. In this respect wombats are an anomaly; they are the only large (35 - 40 kg) Australian

herbivore (and the only large marsupial) to utilise the hindgut digestive strategy, and the only marsupial to use true colon fermentation.

Reasons why some digestive strategies seem to be better at certain body sizes have been put forward by several workers (Janis 1976; Demment and Van Soest 1985; Hume 1989; Illius and Gordon 1992). Much of this attention has focused on why the ruminant strategy both dominates, and is confined to, middle-sized herbivores. Most ruminants and other medium-sized herbivores are grazers or mixed grazers/browsers, obtaining much of their energy from plant cell walls. There is evidence that these ruminant herbivores have digestive efficiencies on low-fibre foods similar to hindgut fermenters, but on high-fibre foods (such as grasses) rumen fermentation extracts nutrients more efficiently because of the selective retention (and hence prolonged fermentation) of less-digestible components (Janis 1976; Demment and Van Soest 1985). There is also limited evidence to suggest that, even for the same digesta retention time, hindgut fermenters (Owen-Smith 1988) and (macropodid) foregut fermenters (Hume 1982) are less efficient at digesting cell walls than are ruminants. However, the greater food intake and faster rate of digesta passage in non-ruminants probably means that they are able to maintain a similar rate of absorption of energy and nutrients as do ruminants, despite their lower digestive efficiency (Janis 1976). Why the rumen strategy appears to be the 'superior' adaptation amongst middle-sized herbivores then, is not immediately clear. Janis (1976) suggests that this may be due to the efficient use of protein by recycling urea back to the gut microbes, and the ability of ruminants to subsist on less food, which would be an advantage when food resources are limiting. She also points out that on high fibre diets, ruminants may be at a disadvantage compared to similar sized non-ruminants such as horses. This is because non-ruminants should be able to maintain or increase the rate of digesta passage on high fibre diets whereas rate of passage decreases in ruminants due to the sieve-like effect of the rumen. Thus, for a ruminant, there is a threshold in the fibre content of the diet, above which it would be unable to support itself. Hindgut fermenters have, in fact, also been shown to decrease their intake on high fibre foods, but not to the extent of ruminants (data from Foose 1982 presented in Owen-Smith 1988). Illius and Gordon (1992), using a simulation model, concluded that the higher food intake rates of hindgut fermenters may result in them obtaining more

energy from food than do similar-sized ruminants when both utilise abundant foods of the same quality. Therefore, under conditions of abundant food resources hindgut fermenters should dominate. Similar to Janis (1976), they suggested that the predominance of ruminants amongst middle-sized herbivores is due to their more efficient use of resources under conditions of resource depletion, rather than a superior ability to extract energy from abundant food.

Demment and Van Soest (1985), extending the ideas of Janis (1976) and others, suggest two reasons why the ruminant digestive strategy is not found in very large herbivores. The large absolute energy requirement of large herbivores constrains them to diets with very high contents of structural tissues, such as the leaves of woody dicots (trees and shrubs). Because a large proportion of this diet is effectively indigestible to the herbivore (the energy extracted does not balance the cost of digesta retention time) or is nutritionally inert, selective retention of these fibrous components (as occurs in the rumen) would be disadvantageous. Secondly, larger body size means longer digesta retention time (due to longer gut length) and lower mass-specific energy requirements (lower metabolic rate per unit mass). It is probable that above a certain body size, the combination of increased digesta retention time and lower relative energy requirements relax the need for selective retention. Illius and Gordon (1992) disagree, as their model suggests that the lower digestive efficiency in hindgut fermenters on very high fibre diets is as disadvantageous as the long fibre-retention time in ruminants, and therefore the reason for an upper body-size limit to rumination remains unexplained. Illius and Gordon (1992), however, do not explicitly address the strategy of using the 'duplex' nature of high fibre food resources. A feeding strategy open to hindgut fermenters is to have a high intake of food resources consisting of a mix of easily digested carbohydrates and indigestible fibre (such as leaf and stem). What is easily digested is digested and the remainder is simply shunted through the system to make room for more material. This seems to be the strategy adopted by grazing equids and very large browsing herbivores such as elephants, and small caecum fermenters such as lagomorphs and certain rodents (Owen-Smith 1988).

Demment and Van Soest (1985) suggest that a lower body-size threshold exists for the ruminant digestive strategy because small animals are constrained to rapidly

digestible, low fibre diets and so would gain no advantage having mechanisms for highly selective retention of fibrous material. These workers point to the fact that small ruminants function less like 'classic' ruminants by having less selective retention and more rapid passage of digesta, and deriving proportionately more energy from gastric digestion than do larger ruminants (see also Hoppe 1977).

Reasons for the dominance of hindgut fermentation over non-ruminant foregut fermentation in small and very large body sizes have received less attention. Presumably, the use of either strategy is dependant upon the trade-off between extracting more energy from the easily fermentable carbohydrates (hindgut fermentation) versus use of the nutrients synthesised by gut microbes (foregut fermenters) (Demment and Van Soest 1985; Hume 1989). Small herbivores probably use the hindgut strategy because they are constrained to high quality food items containing a high proportion of easily fermentable carbohydrate and which are also likely to be nutritionally more balanced than lower quality foods. In addition, small caecal fermenters have developed coprophagy to help counteract high faecal nutrient loss. The ability to obtain nutrients from food (determined by gut volume) and the storage capacity for absorbed nutrients (deposits of fat, glycogen and protein) scale approximately isometrically with body size, whereas the mass-specific requirements for nutrients decrease as body size increases (Demment and Van Soest 1985). Because of their relatively lower nutrient requirements, the use of the hindgut strategy in very large animals may reflect a relative advantage of using more efficient extraction and storage of energy from the easily-digestible component of the diet at the expense of obtaining synthesised nutrients, as implied by Demment and Van Soest (1985).

### ***Wombats: a unique adaptive syndrome?***

The first hint that wombats might exhibit energy conservatism came from Wells (1973) who found that southern hairy-nosed wombats *Lasiorhinus latifrons* under laboratory conditions had low basal metabolic rates (BMR). Nitrogen balance experiments also suggested low nitrogen requirements and hence low energy requirements (Wells 1973). Wells (1973) found that water turnover rates of free-living southern hairy-nosed wombats were very low, an indication that field metabolic rates

were also probably low. Barbosa *et al.* (1993) confirmed the low nitrogen requirements of captive southern hairy-nosed wombats and common wombats *Vombatus ursinus*. Johnson (1991a) found that northern hairy-nosed wombats *Lasiorhinus krefftii* were extremely conservative in their ranging behaviour and activity.

In addition to low basal metabolic rate, low rates of water turnover, low nitrogen requirements and low levels of daily activity, wombats possess other adaptations which suggest energy conservatism within these genera, such as fossoriality, large body size, and the ability to survive on poor quality food. The significance of some of these adaptations for energy conservation are discussed below.

Burrowing is an important means of reducing energy expenditure by allowing animals to escape daily temperature extremes, thereby reducing the energetic cost of thermoregulation. If the burrow provides a thermally neutral zone, thermoregulation costs will be minimal for an whilst the endotherm is in the burrow. This is exemplified by the fact that most small desert mammals are fossorial (72%) whereas burrowing is relatively rare amongst small mammals in more temperate habitats (6%) (Bradley and Yousef 1972). Burrows also provide a physical refuge from predators, allowing animals to spend long periods inactive. Large body size and the use of burrows are likely to confer significant advantages in reducing energy expenditure. Recently, Johnson (1998) reviewed the influence of body size and diet on fossoriality. Burrowing is more common amongst smaller than larger animals, and is rare above about 10 kg. At an adult weight of 25 to 40 kg, wombats are the largest burrowing herbivores. The only larger animal to regularly use self-dug burrows is the armadillo *Oryzomys affinis*, an insectivore. The next largest burrowing herbivores are the porcupines, but which differ from Vombatids by eating mostly foods concentrated in energy and nutrients such as storage organs. The nearest burrowing/grazing analogue to the Vombatids are the marmots, vischard and mara, at mean body masses of about 5 kg. The Vombatids, therefore, are almost a magnitude greater in body size than their nearest analogues.

The corollary of energy conserving strategies is a reduced requirement for energy from food. The observed low requirements for nitrogen (protein) by common wombats and southern hairy-nosed wombats (Barbosa *et al.* 1993) mean that wombats should be able to expand their dietary niche to include lower quality (higher fibre) foods than would

be expected for their body size. The powerful dental mill of wombats (indicating thorough comminution of cell walls and release of the soluble cell contents) and the use of a hindgut fermentation strategy indicate that wombats are maximising the extraction of energy from cell contents, at the expense of nutrients synthesised by gut microbes. To my knowledge, coprophagy has not been observed in wombats. This is plausible, since animals that use this strategy are caecal fermenters, whereas wombats are colon fermenters. Southern hairy-nosed wombats are also able to utilise dry foods even without access to free water (Gaughwin *et al.* 1984), a consequence of their low water turnover rate (Wells 1973).

Wombats live in seasonal or intermittently productive environments in which food quality and availability fluctuate strongly. It is probable that wombats have strategies to cope with declining food quality during poor seasons, as has been shown in other species (eg Jarman and Sinclair 1979; Owen-Smith 1988). Such strategies include attempting to maintain dietary quality through increased selectivity for high quality food items, maintaining or increasing rates of food intake by accepting a lower quality diet, using body reserves, decreasing energy expenditure, or some combination of these. Smaller herbivores are better able to increase their selectivity for higher quality items because of the morphology of their mouths and their lower absolute energy requirements. The only practical method for larger herbivores attempting to maintain dietary quality is to select feeding areas which contain a greater proportion of higher quality food items. This may be through increasing home range size or by moving to a new area. Moving to a new location is not an option for wombats because of their use of permanent burrows. Wombats, therefore, are dependant solely upon the food resources within their home range during all seasons. Wombats might expand home range size in response to declining food quality, though this is also likely to be energetically more expensive due to the extra distance travelled from the burrow. Rather than increasing selectivity, an alternative option for larger animals is to attempt to maintain a high rate of intake of lower quality food and to use fat reserves stored during good seasons. Compared to smaller herbivores, large herbivores are probably better able to accumulate fat stores because of their lower mass-specific energy requirements. Moreover, their lower mass-specific metabolic rate means that fat reserves also last longer during poor seasons than

those of smaller animals. Storing energy during good seasons for use during poor seasons would seem to be a viable strategy for wombats. Their hindgut fermentation strategy is suited to maximising the efficiency of energy extraction from high quality food (containing a large proportion of soluble carbohydrates) during good seasons, and their low energy expenditure means that stored energy reserves are used at a slower rate and therefore last longer during the poor season. Such a strategy would be an advantage in situations where abundance as well as quality is limiting during poor seasons. Theoretically, a further option open to wombats during the poor season is to maintain high rates of food intake (where food is abundant) and to select 'duplex' food resources, using the colon fermentation strategy to maximise the efficiency of energy extraction from the easily digested component of the diet (and to simply shunt the fibrous material through the digestive tract largely undigested).

Some of the adaptations possessed by wombats are either unique amongst mammals, or are unique amongst marsupials. These include being the largest burrowing herbivores, the only marsupials to possess continuously growing incisors *and* molars, the only marsupials to possess a single pair of upper incisors (similar to rodents) and the largest marsupials to have a hindgut fermentation strategy. Wombats are unique amongst the endemic Australian fauna in being the only large grazers to utilise the hindgut strategy (all other large grazers, the kangaroos and wallabies, use foregut fermentation), and the only Australian herbivores (and marsupials) to use true colon fermentation. This combination of adaptations appears to be unique amongst mammals, suggesting that wombats might have a unique adaptive syndrome for energy conservation.

The following is an hypothesised adaptive syndrome for wombats:

1. The combination of large body size, use of burrows, low metabolic rate and energy-conservative behaviour enables wombats to exist in climatically harsh habitats and to 'bend the rules' to expand their dietary niche to include food items of lower quality than expected for their body size.
2. Their dietary strategy for coping with seasonal declines in food quality is to maximise the efficiency of energy extraction from foods during the good season (through hindgut fermentation). Instead of than maintaining dietary quality

through increased feeding selectivity during poor seasons, wombats maintain food intake, exploit the duplex nature of foods and use the stored energy reserves to make up for any shortfalls in energy intake from food of low quality or low abundance.

3. They cope with reduced energy intake during seasons of poor food quality by reducing energy expenditure, and this is achieved by decreased activity levels.

### ***Aims and Organisation of this thesis***

The aim of this thesis is to examine and quantify aspects of the energetics and nutritional ecology of free-living wombats. It is my hope that this study will reveal the extent of energy conservatism amongst the Vombatidae, provide insights into the strategies used to minimise energy expenditure and, in part, reveal their adaptive syndrome. A secondary aim is to increase our understanding of the ecology of the Vombatids, a relatively unstudied group which has one species on the brink of extinction.

I have divided the thesis into the examination of a number of hypotheses or factual expectations:

#### Food Resources

1. Biomass of food resources decline during poor seasons.
2. Nutritional quality of food resources decline during poor seasons.

#### Feeding Ecology

3. The areas that wombats select for feeding within their home range differ between good and poor seasons.
4. Wombats increase selectivity for high quality food items during poor seasons.
5. The digestive efficiency of wombats decreases during poor seasons.

#### Home Range and Activity

6. Home ranges (or ranging within the home range) contract during poor seasons.
7. Overall activity levels are lower during poor seasons.

#### Energetics

8. Field metabolic rates are lower than the 'mammalian standard' for their body size.
9. Water turnover rates are lower than expected for body size.
10. Wombats expend less energy during the poor season than the good season.
11. Wombats do not maintain energy balance during poor seasons.

Explanation of these hypotheses is organised into 4 separate chapters: Chapter 4 deals with food resources, diets and feeding selectivity; Chapter 5 covers habitat use, home ranges and activity; water metabolism is considered in Chapter 6; and field energetics and activity are discussed in Chapter 7. This chapter and the following chapter give a theoretical background to ecological energetics and provide information on the taxonomy, evolution and ecology of the Vombatidae. Chapter 3 gives details of the study sites and an overview of the methodologies used. The final chapter (8) re-examines the hypotheses outlined above and synthesises the findings of this study.

## CHAPTER 2

# ECOLOGY AND EVOLUTION OF THE VOMBATIDAE

### 2.1 INTRODUCTION

This chapter provides background on the ecology, current distributions, and taxonomy of the three species of wombat. The evolution of the Vombatidae within the Australian mammal fauna is compared to that of ecologically similar eutherian herbivores of other continents in the context of changing environments and energetic constraints imposed by food resources. Unless otherwise stated, information was synthesised from Archer (1981, 1984); Hope (1984); Kirsch (1984); Martin (1984); Janis (1989, 1993); Archer *et al.* (1991) and Murray (1998).

### 2.2 MORPHOLOGY AND ECOLOGY OF WOMBATS

The three extant species of wombat are terrestrial, fossorial, herbivorous marsupials endemic to Australia. Adults of all three species weigh around 25 kg to 35 kg but can reach 40 kg, and are the largest burrowing herbivores. They are powerfully built animals, with short muscular limbs, short necks and large, broad heads. The front paws have stout, flattened claws and are used for excavating burrows. The tail is reduced to a vestige hidden by body fur. Wombats have rootless, continuously growing incisors *and*

molars, a characteristic unique amongst marsupials and found only in some of the Rodentia (eg. beavers, pocket gophers). Another characteristic of wombats that is unique amongst marsupials is the reduction of the upper incisors to a single pair. Wombats also have heavy skull and jaw bones and large jaw muscles. The characteristics of the skull, jaw muscles and dentition indicate a powerful grinding mechanism. Common wombats *Vombatus ursinus* (*Vombatus* from the aboriginal word 'wombat', *ursinus* = bear-like) have bare granular skin on the nose and are covered with coarse fur which varies from dark grey to red/brown. The ears are small, thick, rounded and furred. Northern hairy-nosed wombats *Lasiorhinus krefftii* (*lasios* = hairy, *rhis* = nose, *Krefftii* from Kreft) and southern hairy-nosed wombats *L. latifrons* (*latus* = broad, *frons* = forehead) are similar in appearance to each other and contrast to the common wombat in having broad cow-like muzzles covered with velvety fur, and soft, grey (sometimes brown) body fur, often with darker patches around the eyes. The ears are thinner, larger and less furred than those of common wombats.

Wombats are nocturnal, sheltering in deep burrows during the day and emerging at night, though they occasionally emerge during the day in winter to bask or graze. The period spent above ground varies from three to eight hours in a night (McIlroy 1995). Burrows are up to 20 m long (McIlroy 1995), may have nesting chambers containing leafy bedding material and may have multiple entrances. The diet consists of mostly native grasses, but also includes sedges, rushes and the roots of shrubs and trees (Mallet and Cook 1986; McIlroy 1995).

The first European description of a wombat came from a specimen found in 1797 on Clarke Island in Bass Strait (Troughton, 1941). Wombats were later found on most islands in Bass Strait and on the mainland. A letter accompanying the first specimen sent back to England noted its similarity to a badger, and that Aboriginals called it 'wombach'. All three species have suffered range contractions since European settlement. The northern hairy-nosed wombat, though apparently not abundant at the time of European settlement, is currently listed as endangered (IUCN 1994) and exists as less than 70 individuals with a total distribution of 300 ha. Common wombats and southern hairy-nosed wombats are still widely distributed and abundant, though continuing range contractions and population declines may change this situation.

## 2.3 DISTRIBUTIONS

Distributions of the three species of wombat are allopatric, and differ markedly in habitats and climate. Common wombats are now found mostly in temperate, mesic and usually mountainous areas of south-eastern Australia (Fig 2.1). Their main habitats are forest covered, but other habitats include scrubs and coastal heath in southern parts of its range. Interestingly, the geographical limit of common wombats extends west into dryer country and almost to the edge of the distribution of the Southern hairy-nosed wombat (though populations of common wombats in this area are small and fragmented). In contrast to common wombats, the two hairy-nosed species occur in arid and semi-arid habitats. Northern hairy-nosed wombats are found in semi-arid open tropical woodland in central Queensland. Southern hairy-nosed wombats inhabit the largely treeless arid and semi-arid plains of southern Australia which lie within the dry Mediterranean climatic zone.

## 2.4 TAXONOMY OF THE VOMBATIDAE

### 2.4.1 Modern Taxonomy

The three extant species of wombat belong to the Order Diprotodonta within the Subclass Marsupialia. This Order is characterised by marsupials that have only one pair of functional incisors in the lower jaw. It is a diverse and successful group, comprising the kangaroos, possums, wombats and the koala. Wombats and the koala are placed together in the Suborder Vombatiformes, reflecting their relative similarity and apparent early divergence from the other species in this Order. Within the Suborder Vombatiformes, the Family Vombatidae contains the two extant genera of wombats; *Lasiorhinus* (the hairy-nosed wombats) and *Vombatus* (the naked-nosed common wombat). Three subspecies of the common wombat are currently recognised; *V. u. hirsutus*, *V. u. ursinus* and *V. u. tasmaniensis*.



**Figure 2.1** Distributions of the three species of wombat.



**Plate 1**

Common wombat burrow in Riamukka State Forest on the Great Dividing Range of New South Wales. Burrows are usually single entrance and may be used by several individuals at different times



**Plate 2** Southern hairy-nosed wombat burrows at Brookfield Conservation Park in South Australia. Burrow entrances are restricted to fissures in the hard calcrete layer and are interconnected to form warrens.



**Plate 3** Northern hairy-nosed wombat burrow at Epping Forest Scientific Reserve in Queensland. Burrows often have more than one entrance.

### 2.4.2 Previous wombat forms

At least ten species of wombat have been described from late Oligocene, Miocene, Pliocene and Pleistocene fossil remains found at various sites throughout Australia (Archer 1984). Three of these species are large forms and have been described by Owen (1877). Subsequent taxonomic revisions have resulted in these being named *Phascolomys medius*, *Ramsayia magna* and *Phascolonus gigas*. The largest of these 'giant' wombats, *Phascolonus gigas*, has a skull the size of a cow and was several times the size of modern wombats. The giant wombat forms probably originated in the early Pliocene and appear to have been widespread (Murray 1998). One of the earliest wombat fossils (*Rhizophascolonus crowcrofti* from the Miocene, ca. 23 million years ago or mya) has rooted teeth, suggesting that it is an ancestral form. The most recent fossil (*Vombatus hacketti* from the late Pleistocene) has a form similar to that of the modern common wombat. *Warendja wakefieldi* is another 'recent' Vombatid, also known only from the late Pleistocene. Murray (1998) believes that *Warendja* represents a survival from a primitive wombat lineage, and therefore might represent the ancestral wombat form. *Vombatus* first appears in late Miocene/early Pliocene assemblages from South Australia (Pledge 1992 cited in Murray 1998) and *Lasiorhinus* is present by mid Pliocene. Interestingly, fossil wombats have not been found in New Guinea despite its connection with Australia during the Miocene. In addition to the formally described Vombatids, numerous Vombatid fossil fragments remain unassigned and may represent undescribed species. Clarification of taxonomic relationships amongst early Vombatid has been impeded by the continuously growing teeth which are well-worn and lack morphological information for phylogenetic analysis. Indeed, Murray (1998) considers the two *Lasiorhinus* spp. to represent the opposite ends of an interrupted geographic cline.

## 2.5 EVOLUTION OF MODERN MAMMALIAN HERBIVORES

### 2.5.1 Evolutionary Patterns and Climate Change

The Cenozoic Era, from 66 million years ago (mya) to the present, is commonly known as the ‘Age of Mammals’ since in this era, after the demise of the great reptiles, mammals diversified and flourished. Evolutionary trends among mammals appear to have been profoundly influenced by changing climates, largely via its effect on habitat and food resources, and geographical separations. The fossil record of these climatic changes, in both the fauna and flora, is much better preserved in the northern hemisphere than in the southern continents, including Australia, which largely remained above sea level and hence escaped major depositional events.

Fossil remains of fauna and flora during the Early Paleocene (ca. 66 mya) suggest wetter, more luxuriant environments than occur in the same areas of the world today. Australia, Antarctica and South America were joined and lay at higher latitudes, and had become separated from Africa. At this time the northern hemisphere continents of Europe, Asia and N. America formed one large continent (Laurasia). The world had a warm, equitable climate with little latitudinal variation. Closed-canopy tropical and sub-tropical forests, sub-tropical woodlands and broad-leafed deciduous forests were widespread. The Early Paleocene mammals present represent ‘archaic’ groups: mainly small, arboreal, forest-adapted forms. Dental morphology points to these mammals being generalist omnivores, with no specialised folivores present. Early Paleocene mammals present on the northern hemisphere continent include didelphoid marsupials, an early pre-ungulate form (Condylarthra), insectivorous “Protoeutherian” forms and various squirrel-like animals including “Protoprimate” forms. During the Paleocene, a few larger, ground dwelling, more herbivorous forms developed, including wombat-like taeniodonts and tillodonts, sloth-like or hippopotamus-like pantodonts and the (possibly semi-aquatic) rhinoceros-like uinatheres. Smaller, ungulate (ie. hooped eutherian) herbivores appeared in the Late Paleocene (ca. 58 mya). The Paleocene record is sparse for the southern continents of Gondwanaland and Africa (and is missing entirely for Australia). By the Late Paleocene, early monotremes were already present in South America and Australia, and a diversity of marsupials (mostly didelphoid and borhyaenoid) were present in South

America. It is not known when the first marsupials appeared in Australia (the oldest known fossil is a post-Paleocene platypus-like marsupial), though it is generally assumed that they immigrated from South America via Antarctica.

Floral and faunal assemblages during the Eocene (ca. 37.5-55 mya) indicate the expansion of tropical forests towards the poles, but an opening up of the understorey in lower latitudes. This period was marked by a high rate of turnover in faunal groups; many new mammal groups appeared, particularly amongst ground dwelling mammals, and many forest-adapted groups declined or became extinct. Mammalian herbivores during the Early Eocene were still predominantly frugivorous/omnivorous, though this period saw the appearance in the northern hemisphere of the first terrestrial browsers, primarily early forms of the perissodactyl and artiodactyl ungulates. The perissodactyls were diverse and abundant over much of the northern hemisphere continent during the Early Eocene, comprising the extant lineages of equids, rhinoceros and tapirs, and several extinct lineages. In contrast, artiodactyl diversity was restricted to small, and still predominantly omnivorous forms. In South America, arboreal and scansorial omnivorous and insectivorous marsupial forms declined (despite an overall increase in marsupial diversity) and diversity and abundance increased amongst placental ground dwelling omnivores and herbivores (mainly armadillos and ungulates). The fossil record is sparse for Australian Eocene fauna, though marsupials were probably mainly arboreal and omnivorous, and a placental (a pre-ungulate condylarth) was possibly present.

The Late Eocene (38 to 42 mya) encompassed the greatest climatic change of the last 66 million years, and began the unidirectional climate shift that continues to the present. Changing positions of the continents (Australia was breaking away from Antarctica and drifting north), changing ocean circulation patterns and a cooling world climate combined to produce increasing aridity and, for the higher latitudes, an increase in seasonality. Tropical forests were contracting and temperate forests and woodlands were spreading. A climatically more complex world was producing a more diverse and heterogeneous vegetation, and mammals were diversifying into the vacant 'adaptive space' of the new habitats. Many of the forest-adapted groups, particularly arboreal specialised frugivores, declined in diversity and became extinct or restricted to the tropics. This was probably related not so much to cooler temperatures per se, but to

increased seasonality in fruit production and a trend towards hard fruit and small-sized seeds. Dental morphology of the remaining frugivorous groups suggests a dietary shift from soft fruit to hard fruit. Many ancient ground-dwelling omnivore/herbivore groups suffered declines or extinctions, such as the pre-ungulate condylarths, the wombat-like taeniodonts and tillodonts, and the rhinoceros-like uinatheres. The mammalian herbivores that radiated into the new habitats of the northern hemisphere continents were primarily ungulates, of which the artiodactyls soon dominated in both diversity and abundance. Artiodactyls comprised three distinct lineages: the (still largely omnivorous) suines (pigs and relatives), tylopods (camels and relatives) and ruminants. Perissodactyls remained a prominent component of the fauna, despite their decline in diversity and abundance, and were represented by mainly tapiroids, rhinocerotoids and (tapir-like) palaeotheres. The equids suffered major declines during the Late Eocene and almost became extinct. During this period there was a trend for increasing upper body size in most mammalian groups, particularly amongst ungulates, and a trend for a more cursorial (longer legged) body form. Dental morphology of the larger body size taxa suggest that they were more folivorous than the smaller and more omnivorous taxa. Unfortunately, little is known of the effects of this period on the faunas of the southern continents of Africa, Australia, South America and Antarctica.

The continuing trend of decreasing temperatures and increasing aridity during the Oligocene (23- 34 mya) and Miocene (5 to 23 mya) resulted in the contraction of tropical forests to less than present day levels, having been replaced by various woodland types (subtropical, temperate broad-leafed deciduous, temperate coniferous), scrubs and dense 'woody savannas'. Although early grasses had appeared in North America during the Late Eocene, the sparse understorey of the woody savannas was apparently dominated by non-graminoid herbs. The first open savanna-type grasslands probably appeared in the Late Miocene (mostly in east Africa and the Americas), coincident with the first C<sub>4</sub> grasses, but modern-type grasslands may not have existed until the Pleistocene (1.9 mya). The trend for generally larger body size amongst mammalian herbivores continued, though interestingly, the highest rates of extinction appear to have been amongst the larger body sizes. The most abundant ungulates were woodland-adapted, browsing artiodactyls that resembled modern-day capybaras.

Most of the present-day taxonomic groups of mammals were present by the Miocene, and low sea levels during this period allowed extensive faunal interchange between Africa, Eurasia and North America. The herbivorous mammals of the expanding savannas showed evidence of increased open-habitat adaptations and a trend from browsing to mixed browsing and grazing, as indicated by increasing hypsodonty. The trend for increasing upper body size for many groups also continued. In the northern hemisphere and Africa, artiodactyl ungulates diversified and increased in abundance, and included the appearance of many larger-sized, horned pecoran ruminants, such as bovids (antelope and cattle), cervids (deer) and giraffoids. Increased hypsodonty in molar teeth in bovids suggests a trend towards grazing. Bovid became increasingly prominent in Africa during the Late Miocene, with the appearance of present-day grazers such as wildebeest. Very large browsers, such as modern elephants, also appeared during this period. Pigs and their relatives diversified and included specialised browsing forms, and smaller rhinoceros were replaced by larger, more modern types. Perissodactyl diversity was low, but they were still a prominent component of the fauna. During the Miocene, two major dispersals of perissodactyls occurred from North America to the other continents; firstly the early *Anchitherium* horses, which were then replaced by a dispersal of hipparionid horses. The first true equine horse (*Merychippus*) also appeared at this time in North America. Many mammal groups declined or became extinct during the cooler and drier Late Miocene. Extinctions are particularly noticeable amongst browsing taxa such as the *Anchitherium* horses (which increased in size during the Miocene but were extinct by the end of the period), rhinoceros and smaller ruminant or ruminant-like artiodactyl groups. In South America, cooling and aridification produced a mixture of wooded and open habitats. Larger caviomorph rodents, ground sloths and notungulates diversified whilst diversity declined amongst of forest-adapted groups such as tree sloths and primates. Browsing ungulates also declined during this period except for some large, highly hypsodont (browsing/grazing) species.

The mammalian fossil record for Australia is much more detailed for the Miocene than for the previous epochs. The degree of cooling and aridity which affected the northern latitudes during the Eocene and Oligocene did not appear to have occurred in Australia until closer to the Miocene. Thus, the faunal turnover from tropical forest-

adapted species to open-habitat adapted species which had occurred in other continents was not pronounced in Australia until the Miocene. Australian rainforests at the start of the Miocene had begun to contract, being replaced with forests and woodlands with sclerophyllous components. The faunas that existed during the Early Miocene appear to have consisted largely of forest-adapted marsupials (rodents did not arrive until the end of the Miocene, ca. 5 mya). Most of the present day groups (Families, subfamilies and some genera) of marsupials and the monotremes were represented (in many cases by ancestral forms), together with taxonomic groups which have since become extinct. [Modern groups not represented in the current Miocene fossil record include the numbats (myrmecobiids) and honey possums (tarsipedids), but this is probably an artefact of the fossil record.] Many species were arboreal, and included a diversity of ancestral possums and cuscuses (petaurids, burramyids and phalangerids), and phascolarctids (ancestral rainforest forms of the koala). Ground-dwelling herbivorous marsupials included early forms of the (omnivorous) bandicoots (perameloids), various macropodoid forms (small hopping macropodid balbarines and potoroids) and the sheep-sized (and now extinct) diprotodontoids. An ancestral form of wombat *Rhizophascolonus crowcrofti* was also present. Dental morphology and the paucity of grasses in these forested habitats suggest that mammalian herbivores at this time were predominantly browsers. By the end of the Miocene (5 mya), rainforests were present as only pockets: grasses were prevalent and drier and more open habitats such as eucalypt forests, woodlands and savanna were widespread. A number mammal groups, such as possums, cuscus, marsupial lions (thylacoleonids), and diprotodontids, had declined or become extinct by the end of this period. [Remnants of Miocene flora and fauna groups still persist in the highland forests of New Guinea and in some rainforests in Australia.]

During the Pliocene (1.9 to 5 mya), modern-type deserts formed, grasses were the dominant floral element in the higher latitudes, and arid temperate habitats such as prairie, steppe and pampas were present. Faunal interchange occurred between North and South America, and between North America and Africa via Eurasia. Extant monodactyl equine horses radiated from North America and replaced the hipparionid horses of Asia, Europe and Africa. Edentates, caviomorphs and didelphids radiated from South to North America, and ungulate groups such as peccaries, camelids, deer, tapirs and horses moved

from North to South America. Around 50% of the bovid fauna were now grazers. Spreading of Australian grasslands during the Pliocene coincide with the appearance of the first Australian grazing mammals. These grazers were descendants of the small macropodoid, larger diprotodontoid, and vombatid forms. Each group, though particularly the small macropodoids, underwent rapid radiation to give rise to a diversity of grazing marsupials. At least ten species of vombatid forms have been recorded from Pleistocene deposits. During the late Pliocene (3 mya) and Pleistocene (10,000 ya to 2 mya) the upper range for body size of herbivorous mammals markedly increased, a phenomenon that was world wide. Diprotodontoids ranged from the size of small sheep to the largest marsupial known, the rhinoceros-sized *Diprotodon optatum*. The macropodoid group gave rise to several types of 'giant', short-faced sthenurine kangaroo, and the largest vombatid *Phascolonus gigas* was the size of a small cow. Reasons for the extinction of the Australian megafauna and large-scale extinctions in other parts of the world during the late Pleistocene are still the subject of debate. In Australia and New Guinea, not only did the large diprotodontoids become extinct, but so did the smaller sizes: no diprotodontoids survived past the end of the Pleistocene. The post-Pleistocene Australian grasslands were left to the two remaining groups, the macropodoids and the vombatids, of which the macropodoids were clearly the more successful. Today, there are around 50 macropodoid (kangaroo, wallaby and rat-kangaroo) species and three wombat species. However, while some of the extant kangaroos are near the upper limit of macropodoids of the Pleistocene, the three extant species of wombat are much smaller than some extinct forms. Why two genera of modern wombats were able to survive the upheavals of the Pleistocene when other Vombatid forms and diprotodontoids became extinct, is unclear.

### 2.5.2 Theoretical explanations for evolutionary patterns

The pattern of mammalian herbivore evolution is one of increasing upper body size, a shift from generalist omnivore through browsing to grazing forms, and a shift from gastric digestion to microbial fermentation dominated by the hindgut strategy (non-ungulates and perissodactyl ungulates), and later the foregut strategy amongst middle-sized herbivores. The ruminant foregut strategy (artiodactyl ungulates) dominates

amongst middle-sized herbivores on all continents except Australia, where it is absent. The sacciform foregut strategy, however, emerged as a parallel/convergent adaptation among macropodoid marsupials.

These patterns reflect an evolutionary response to the changing niche (habitat) availability and energetic constraints imposed by food resources. The earliest mammals were small and hence required food concentrated in energy (and other nutrients) to fuel their high mass-specific metabolic rates. Janis (1989) suggests that foliage during the Paleocene probably had little differentiation of cellulose content among structural plant parts and was unavailable as a food resource for small bodied mammals. The shift to general omnivory (most likely insectivory/frugivory) would have been facilitated by larger body size and probably coincided with an increase in the availability of plant parts containing higher concentrations of energy, such as flowers, fruits and young foliage. The trend towards environments containing food resources more fibrous and more diluted in easily digestible energy (such as the expanding woodlands and savannas) or environments where the availability of high quality food resources became seasonal (such as seasonal fruiting in the higher latitudes) would have favoured larger body sizes for herbivores. Increasing body size, as seen amongst the early omnivorous perissodactyl and artiodactyl ungulates, accompanied an expansion of the diet to include more fibrous foods, and a shift from omnivory/frugivory to frugivory/browsing, as evidenced by more hypsodont teeth. The first browsers which radiated into the expanding woodlands during the Early Eocene were mostly larger (but still small by present-day standards) perissodactyls, and these were probably also hindgut fermenters (Janis 1989). Langer (1988) considers fermentation to have initially developed in the hindgut, and so these early perissodactyl browsers were also probably amongst the first herbivores to use fermentation. The smaller artiodactyls were still mainly omnivorous, and so may not yet have evolved fermentation in the forestomach. By the end of the Eocene, however, the artiodactyls were the dominant browsers of the woodlands and 'woody savannas', and may have developed the ruminant digestion strategy.

Why the ruminant system came to dominate whereas the hindgut fermenters (mostly larger sizes such as equids) suffered major declines or extinctions remains to be answered. It has been traditionally attributed to competitive interaction and ecological

replacement of an 'inferior' hindgut fermentation strategy by a 'superior' ruminant strategy, though Janis (1989) suggests that it is due to changing niche availabilities rather than direct competition. The picture is complicated by extinctions amongst both perissodactyls and artiodactyls, diversity and abundance of some perissodactyl groups remaining relatively unchanged (eg. the Rhinoceroidea), and the dramatic decline and recovery of other perissodactyl groups (eg. the Equidae) (Janis 1989). Janis (1989) proposes an evolutionary model based on firstly, the observation that ruminants in the present and in the past show greater diversity in highly seasonal environments whereas hindgut fermenters show greater diversity in environments of low seasonality (Langer 1984; Janis 1989) and secondly, the apparent advantage of the ruminant digestive strategy over other strategies when the availability of food resources is limiting. She suggests that artiodactyls were initially better able to cope with the increased seasonality of the higher latitudes because of their smaller body size and lower absolute food requirements, enabling them to be sustained on a highly selective browsing diet, whereas the remaining vegetation was of too poor quality to be used by the larger hindgut fermenters except for the largest sizes such as Rhinoceroses. The Miocene spread of savanna grasslands was also accompanied by a highly heterogeneous dicot vegetation. The middle-sized hindgut fermenters (such as equids and some rhinoceroses) were able to expand their diet to include fibrous grasses, and the larger hindgut fermenters (such as elephants) increased in size enabling them to utilise low quality browse. The heterogeneous vegetation also provided an ideal environment for the selectively folivorous ruminants, resulting in numerous niches and an increased diversification within this group, with some of the larger sizes eventually becoming selective grazers. Heterogeneity of vegetation (in terms of food quality) is greater in seasonal environments than in tropical environments due to the lower proportion of structural components in the seasonal or ephemeral plant parts, thus promoting diversity amongst selective folivores. Because of their lower food intake, ruminants may also have had an advantage over hindgut fermenters in highly seasonal environments when the seasonal abundance of high quality food items was low. The above rationale also applies to the present-day savanna grasslands which are highly seasonal. Janis (1989) points out that the present-day pattern of high ruminant diversity and lower hindgut fermenter diversity should not be seen as such an 'ecological disaster' for hindgut fermenters, since the difference between

absolute abundances of hindgut fermenters and ruminants is not great, and the current pattern of diversity is expected. In any herbivore system, diversity will be greater amongst selective feeders (such as ruminants) due to the greater niche diversity for this feeding mode than for generalist herbivores, such as equids.

Although the domination of foregut fermentation amongst large Australian herbivores parallels that of the grazing communities in other continents, explanations involving the ruminant digestive strategy do not apply to the non-ruminant Australian foregut fermenters. Reasons for the increase in foregut fermenters and decline of large hindgut fermenters (extinction of the large diprotodonts and decline in diversity of wombats) during the Pleistocene remain unclear. It is possible that the nutrient-poor grasslands of Australia favoured the foregut fermentation strategy of macropods because of the ability to obtain synthesised nutrients. Wombats may have escaped this nutrient constraint through extreme energy conservation and hence low mass-specific nutrient requirements. Why Australian herbivores have not adopted the strategy of using very large body size (the largest extant Australian herbivores weigh less than 100 kg) to lower their mass-specific energy and nutrient requirements, as have herbivores on other continents, is not clear. Indeed, all of the large Pleistocene herbivores (such as the early wombat forms) are now extinct. It is possible that very large herbivores cannot support their large absolute energy requirements on the low biomass and nutrient-poor grasslands of Australia, though this does not appear to be the case with introduced large eutherian herbivores. Camels, for example, survive in habitats that are only intermittently productive.

The present-day pattern of high diversity amongst foregut fermenters (kangaroos) and low diversity amongst the hindgut fermenters (wombats) is probably partly a function of niche diversity and feeding mode, as has been suggested for herbivore communities on other continents. Macropodids come from small, omnivorous or highly selective folivorous ancestors, and present-day macropodids still demonstrate high levels of selectivity for food items (Jarman 1994; Evans and Jarman 1999). These highly selective macropodid herbivores are able to occupy a diversity of niches, whereas wombats are probably more generalist feeders occupying fewer, broader niches. Locally, one wombat's range may overlap with those of 1 to 4 or 5 macropodoid species.