

CHAPTER 7

FIELD ENERGETICS

7.1 INTRODUCTION

In this chapter, I examine a central aspect of this thesis: the energetics of the three species of wombat under free-living conditions in their natural habitats. This is the first study of the field energetics of wombats. Two studies have estimated the ‘standard’ or ‘maintenance’ energy requirements of common wombats (Barboza 1993) and southern hairy-nosed wombats (Wells 1973; Barboza 1993) in the laboratory.

Most knowledge of animal metabolism has come from such laboratory studies, where ‘standard’, ‘basal’ or ‘maintenance’ metabolic rates are measured under standardised conditions, ie. a healthy adult animal resting in a post-absorptive state in its thermoneutral zone (Blaxter 1962). These metabolic rates estimate the minimum energetic cost necessary for maintenance of biological ‘machinery’. Basal metabolic rates (BMR) have commonly been extrapolated to field metabolic rates (FMR) of free-living animals, though this should be done with caution since BMR is not necessarily a reliable index of FMR (Koteja 1991). Field metabolic rate is the total energy expenditure of a wild animal during the course of its daily activities. It includes the costs of basal metabolism, thermoregulation, locomotion, feeding, digestion and food detoxification, reproduction and growth, activity and other expenses that ultimately appear as heat, as well as savings due to hypothermia (Nagy 1987). Field metabolic rate varies as animals

respond to changes in food supply, food quality, predation, reproductive status, weather and other factors that are not experienced by laboratory animals.

The development of the doubly-labelled water technique (Lifson and McClintock 1966) provides a means for the measurement of FMR. The technique, however, is relatively expensive and requires specialised technology, both of which preclude the routine measurement of FMR. The expense of the ^{18}O (oxygen-18) isotope (\$200 per mL at the time of this study) has meant that studies of FMR have involved mostly small animals (< 100 g) since larger animals require correspondingly larger amounts of isotope. Studies of FMR in animals larger than about 10 kg are rare; excluding humans, data are available for only four species (three eutherians and one marsupial), and are limited to a few individuals of each species.

7.2 METHODS

7.2.1 Sampling Procedure

Field metabolic rates were measured in free-living wombats of all three species using the doubly-labelled water technique (Lifson and McClintock 1966; Nagy 1980; Nagy and Costa 1980). Water that has been 'doubly-labelled' has a known proportion of both the hydrogen and oxygen atoms 'labelled' with isotopes. As described in Chapter 6, hydrogen atoms can be labelled with either tritium (^3H) or deuterium (^2H) isotopes. Oxygen atoms were labelled with the oxygen-18 isotope (^{18}O), giving a combination of either $^2\text{H}_2^{18}\text{O}$ (deuterium and oxygen-18) or $^3\text{H}_2^{18}\text{O}$ (tritium and oxygen-18), as opposed to unlabelled water ($^1\text{H}_2^{16}\text{O}$). In practice, both the hydrogen and oxygen atoms are not labelled on the same molecule; doubly-labelled water is a mixture of water containing hydrogen isotopes (either tritiated water or deuterium) and water containing oxygen isotopes. The two types of labelled water can be injected separately (as was done in this study) into the animal and allowed to mix with the body water pool.

The doubly-labelled water technique involves enriching the body water with isotopes of hydrogen and oxygen and then measuring the rates at which each isotope is lost to the environment. Oxygen isotopes leave the body water pool as carbon dioxide

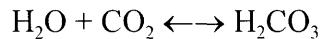
(CO₂) and water (H₂O), whereas hydrogen isotopes leave the body as water only. The rate of loss of labelled H₂O can be used to estimate the rate of water influx and efflux (see Chapter 6). Water efflux gives a measure of the ¹⁸O lost as water and the difference between this and total ¹⁸O loss is equivalent to the amount of ¹⁸O lost through CO₂ production. The rate of CO₂ production can then be used to calculate the metabolised energy expenditure expressed in kJ.

The study areas and methods that I used to capture and handle wombats are described in Chapter 3, and details of the blood sampling, injection and release procedures, and recapture intervals are given in Chapter 6. After obtaining a background blood sample, animals were injected intraperitoneally with 4.0 mL of ¹⁸O isotope (99%+ atoms excess ¹⁸O). At the same time they were injected with either deuterium or tritium for the water turnover measurements (Chapter 6). The doubly-labelled water used for common wombats was a mixture of tritiated water and oxygen-18, and for the two hairy-nosed species was a mixture of deuterium and oxygen-18. The more expensive deuterium was used in the hairy-nosed species because of the stringent permit requirements for the use of radioactive substances in South Australia and to avoid any real or perceived side-effects from the use of radioactive substances in the endangered northern hairy-nosed wombat. Isotope turnover measurements were done on twenty-three wombat individuals, with measurements of some individuals done during more than one season. Samples from common wombats were obtained during the cool dry winter ('poor' season) and warm wet summer ('good' season), samples from southern hairy-nosed wombats were obtained during the cool wet winter ('good' season) and hot dry summer ('poor' season), and samples from northern hairy-nosed wombats were obtained from the warm dry winter ('poor' season), but not the hot wet summer.

7.2.2 Sample Analysis

I extracted water from blood samples using the micro-distillation technique and by vacuum sublimation (both described in Chapter 6). A 50 µl aliquot of the distilled water was then frozen in liquid nitrogen and all remaining gas evacuated. The water sample and a standard charge of CO₂ gas were then heated in Urey exchange tubes at 50°C for 10 hours to allow Urey Equilibration to occur. Urey Equilibration enables the

free exchange of oxygen atoms between the CO₂ molecules and the water molecules (enabling ¹⁸O to be transferred from H₂O to CO₂) via the equilibrium reaction:



The proportion of oxygen atoms introduced to the Urey Tubes as part of the CO₂ gas is negligible compared with the amount of oxygen atoms in the water sample. This means that once oxygen atoms have been freely exchanged between the CO₂ and water sample, the ratio of oxygen-16 ('normal' oxygen) and oxygen-18 isotopes on the CO₂ molecules reflects the ratio of these isotopes in the water sample. The ratios of oxygen-16 and oxygen-18 isotopes on the CO₂ molecules were analysed in an Isotope Ratio Mass spectrometer ('Optima' model, V.G. Isotech, Cheshire England) by comparing the ratio of molecular mass 46 (ie total mass of carbon dioxide carrying an oxygen-18 atom, ¹²C¹⁶O¹⁸O) to molecular mass 44 (normal carbon dioxide mass ¹²C¹⁶O₂) in the CO₂ gas. The ratio of oxygen-18 atoms in the sample was then expressed relative to a standard ratio (Standard Mean Ocean Water, or SMOW).

7.2.3 Calculations

Rates of CO₂ production were calculated using the equations of Nagy (1983). CO₂ production rates can be converted to standard units of energy metabolism (joules) if the energy composition (relative proportions of fat, protein and carbohydrate) of the metabolic substances in the diet are known (Blaxter 1962). Thermal equivalents for CO₂ production from a diet of plant material typically yields 21.8 J per mL CO₂ (Nagy and Martin 1985). CO₂ production rates were converted to joules using the equations:

Mass specific values:

$$\text{kJ} \cdot \text{kg}^{-1} \cdot \text{day}^{-1} = \text{CO}_2 \text{ mL} \cdot \text{g}^{-1} \cdot \text{h}^{-1} \times 21.8 \times 24$$

Absolute values:

$$\text{kJ} \cdot \text{day}^{-1} = \text{CO}_2 \text{ mL} \cdot \text{g}^{-1} \cdot \text{h}^{-1} \times 21.8 \times 24 \times \text{body weight in kg}$$

7.3 RESULTS

7.3.1 Biological Half-life of ^{18}O Isotope

Biological half-life of the ^{18}O isotope during the dry season did not differ significantly between southern hairy-nosed wombats (29.4 ± 4.4 days) and northern hairy-nosed wombats (23.8 ± 1.3 days), but both were significantly longer than in common wombats (9.3 ± 0.7 days) (Kruskal-Wallis $H_{2,14} = 12.39$, $P = 0.002$, Kruskal-Wallis comparison of median rank). No significant differences were found for half-life of ^{18}O between common wombats and southern hairy-nosed wombats during the wet season ($t_8 = -1.03$, $P = 0.33$).

For common wombats, half-life of ^{18}O varied significantly between sexes (males: 8.1 ± 0.6 days; females: 10.4 ± 1.3 days) but not between seasons (ANOVA sex: $F_{1,9} = 7.36$, $P = 0.024$; season: $F_{1,9} = 0.39$, $P = 0.55$). For southern hairy-nosed wombats, half-life of ^{18}O varied significantly between seasons (wet season: 10.1 ± 0.7 days; dry season: 29.4 ± 4.1 days) but not between sexes (ANOVA sex: $F_{1,5} = 1.07$, $P = 0.35$; season: $F_{1,5} = 26.47$, $P = 0.0036$).

7.3.2 Field Metabolic Rate

Field metabolic rates for each species of wombat are given in Tables 7.1 and 7.2 as mass-specific units ($\text{mL CO}_2\text{.g}^{-1}\text{.h}^{-1}$ and $\text{kJ}\text{.kg}^{-1}\text{.d}^{-1}$) and absolute units ($\text{kJ}\text{.d}^{-1}$). Mean seasonal FMR are shown in Figure 7.1. CO_2 production rates in one individual common wombat (female #8) during summer have been excluded from analyses due to the spurious values arising from insufficient isotope turnover. FMR (rates of CO_2 production) did not differ significantly during the dry season between common wombats ($0.297 \pm 0.037 \text{ mL}\text{.g}^{-1}\text{.h}^{-1}$), southern hairy-nosed wombats ($0.254 \pm 0.104 \text{ mL}\text{.g}^{-1}\text{.h}^{-1}$) and northern hairy-nosed wombats ($0.262 \pm 0.017 \text{ mL}\text{.g}^{-1}\text{.h}^{-1}$) (Kruskal-Wallis $H_{2,14} = 1.58$, $P = 0.45$, Kruskal-Wallis comparison of median rank). Similarly, FMR between common wombats ($0.615 \pm 0.100 \text{ mL}\text{.g}^{-1}\text{.h}^{-1}$) and southern hairy-nosed wombats ($0.536 \pm 0.035 \text{ mL}\text{.g}^{-1}\text{.h}^{-1}$) during the wet season were not significantly different ($t_{5,0} = 0.74$, $P = 0.49$). FMR's for common wombats were significantly higher during the wet season than the dry season, but did not differ significantly between sex (ANOVA sex: $F_{1,9} = 0.42$, $P = 0.52$).

0.53; season: $F_{1,9} = 16.30, P = 0.0029$). Similar to common wombats, FMR's for southern hairy-nosed wombats were higher in the wet season, and no significant difference was found between the sexes (ANOVA sex: $F_{1,5} = 1.95, P = 0.22$; season: $F_{1,5} = 9.33, P = 0.028$).

There was a significant correlation between FMR and water influx for the data pooled from all species (linear regression: $r^2 = 0.31, F_{1,25} = 11.01, P = 0.0028$); animals with higher FMR also tended to have higher water influx rates (Figure 7.2). This regression is useful for detecting outliers or spurious values for individuals, but the trend should be interpreted with caution because it is confounded with habitat differences. No significant relationships were found between FMR and body mass for any of the species or for data pooled from all species (Figure 7.3), thus body size did not appear to influence metabolic rate. FMR was not significantly correlated with mass change for the data pooled from all species (Figure 7.4). Within species, FMR was significantly correlated with change in body mass over the energetics periods for northern hairy-nosed wombats (linear regression: $r^2 = 0.81, F_{1,3} = 12.89, P = 0.037$), with individuals having higher FMR losing more weight. FMR was not significantly correlated with change in mass for the other two species.

Figure 7.5 shows the residual variation in FMR for the available data on other mammalian herbivores. (Sloths *Bradypus variegatus* have been excluded from the regression because of their 'outlier' or anomalous value compared to all other mammals). The zero line represents the 'mean' or 'expected' FMR for any given body size. Superimposed on this regression are the residuals (or deviations from the 'expected' rate) for seasonal FMR of the wombats. Wet season FMR for wombats was above the mammalian 'mean' for herbivores, whereas dry season FMR is well below this mean. The difference in FMR between wombats and other mammalian herbivores are discussed in section 7.4.3

Table 7.1 Mass (at initial capture) and field metabolic rates of common wombats during wet and dry seasons. Missing data indicate animals that were not captured or recaptured within a season.

Tag #	DRY SEASON FMR				WET SEASON FMR			
	Mass (g)	CO ₂ mL.g ⁻¹ .h ⁻¹	kJ.d ⁻¹	kJ.kg.d ⁻¹	Mass (g)	CO ₂ mL.g ⁻¹ .h ⁻¹	kJ.d ⁻¹	kJ.kg.d ⁻¹
3	33400	0.383	6692.88	200.39	34000	0.419	7453.51	219.22
5	31600	0.391	6464.45	204.57	-	-	-	-
10	34200	0.411	7354.20	215.04	34600	0.413	7476.42	216.08
13	33800	0.230	4067.36	120.34	-	-	-	-
15	35200	0.100	1841.66	52.32	-	-	-	-
16	38200	0.249	4976.57	130.28	39000	0.614	12528.55	321.24
18	28400	0.331	4918.30	173.18	-	-	-	-
21	32300	0.284	4799.42	148.59	34200	0.960	17177.70	502.27
24	-	-	-	-	25800	0.668	9017.04	349.50

Table 7.2 Seasonal mass (at initial capture) and field metabolic rates of southern hairy-nosed wombats and northern hairy-nosed wombats. Missing data indicate animals that were not captured or recaptured within a season. NHW = northern hairy-nosed wombat, SHW = southern hairy-nosed wombat.

Species	Tag #	DRY SEASON FMR				WET SEASON FMR			
		Mass (g)	CO ₂ mL.g ⁻¹ .h ⁻¹	kJ.d ⁻¹	kJ.kg.d ⁻¹	Mass (g)	CO ₂ mL.g ⁻¹ .h ⁻¹	kJ.d ⁻¹	kJ.kg.d ⁻¹
SHW	1	23600	0.563	6951.65	294.57	22700	0.584	6935.96	305.55
	2	23100	0.16	1933.75	83.71	23500	0.509	6258.26	266.31
	3	23200	0.106	1286.65	55.46	23000	0.648	7797.78	339.03
	4	-	-	-	-	27000	0.482	6808.93	252.18
	5	24600	0.186	2393.95	97.32	23600	0.457	5642.82	239.10
NHW	61	22600	0.309	3653.72	161.67	-	-	-	-
	32	29550	0.29	4483.56	151.73	-	-	-	-
	82	30500	0.258	4117.06	134.99	-	-	-	-
	152	27400	0.236	3383.22	123.48	-	-	-	-
	25	30000	0.215	3374.64	112.49	-	-	-	-

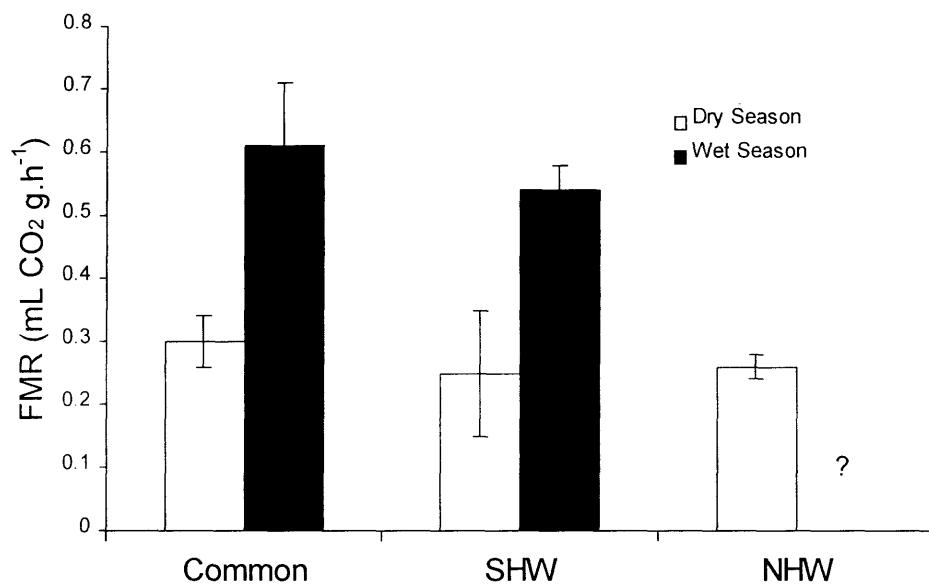


Figure 7.1 Mean seasonal field metabolic rates (FMR) for the three wombat species. Common = common wombat, SHW = southern hairy-nosed wombat and NHW = northern hairy-nosed wombat. Error bars are standard errors.

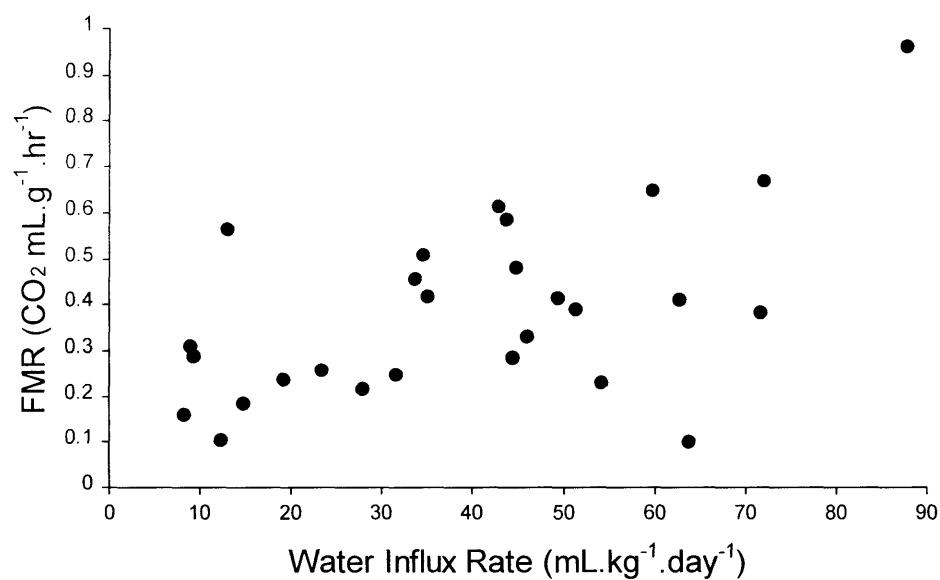


Figure 7.2 Relationship between field metabolic rate (FMR) and water influx rate for all wombat individuals. $y = 0.1885 + 0.005x$. $R^2 = 0.31$

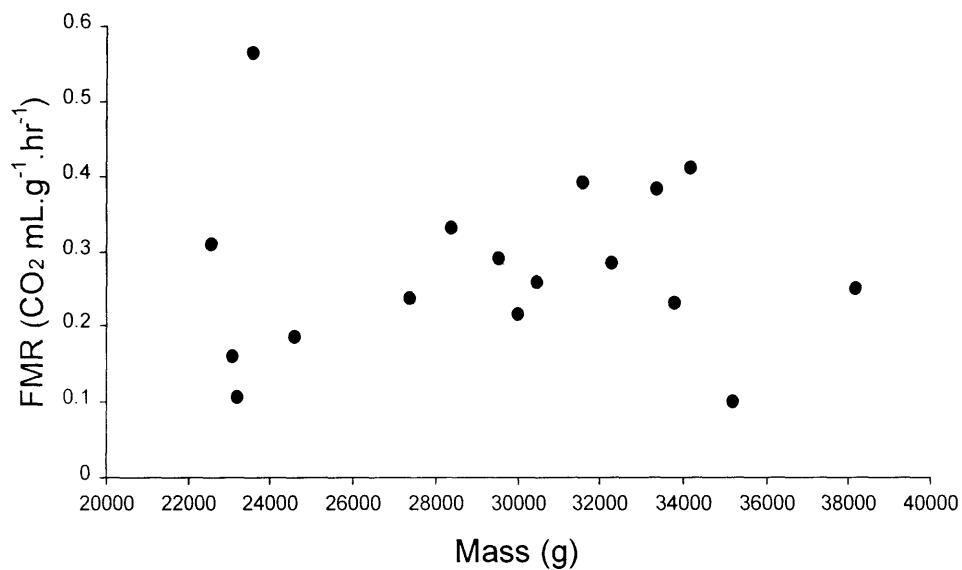


Figure 7.3 Relationship between field metabolic rate (FMR) and body mass for all wombat individuals during the dry season. $y = 0.2615 + 0.00001x$. $R^2 = 0.06$

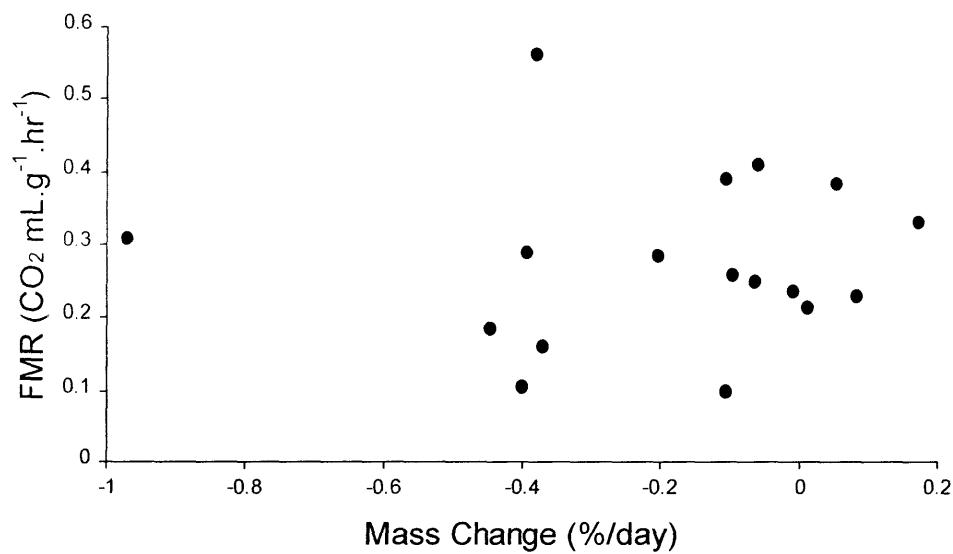


Figure 7.4 Relationship between field metabolic rate (FMR) and body mass change for all wombat individuals during the dry season. $y = 0.2794 + 0.0147x$. $R^2 = 0.001$

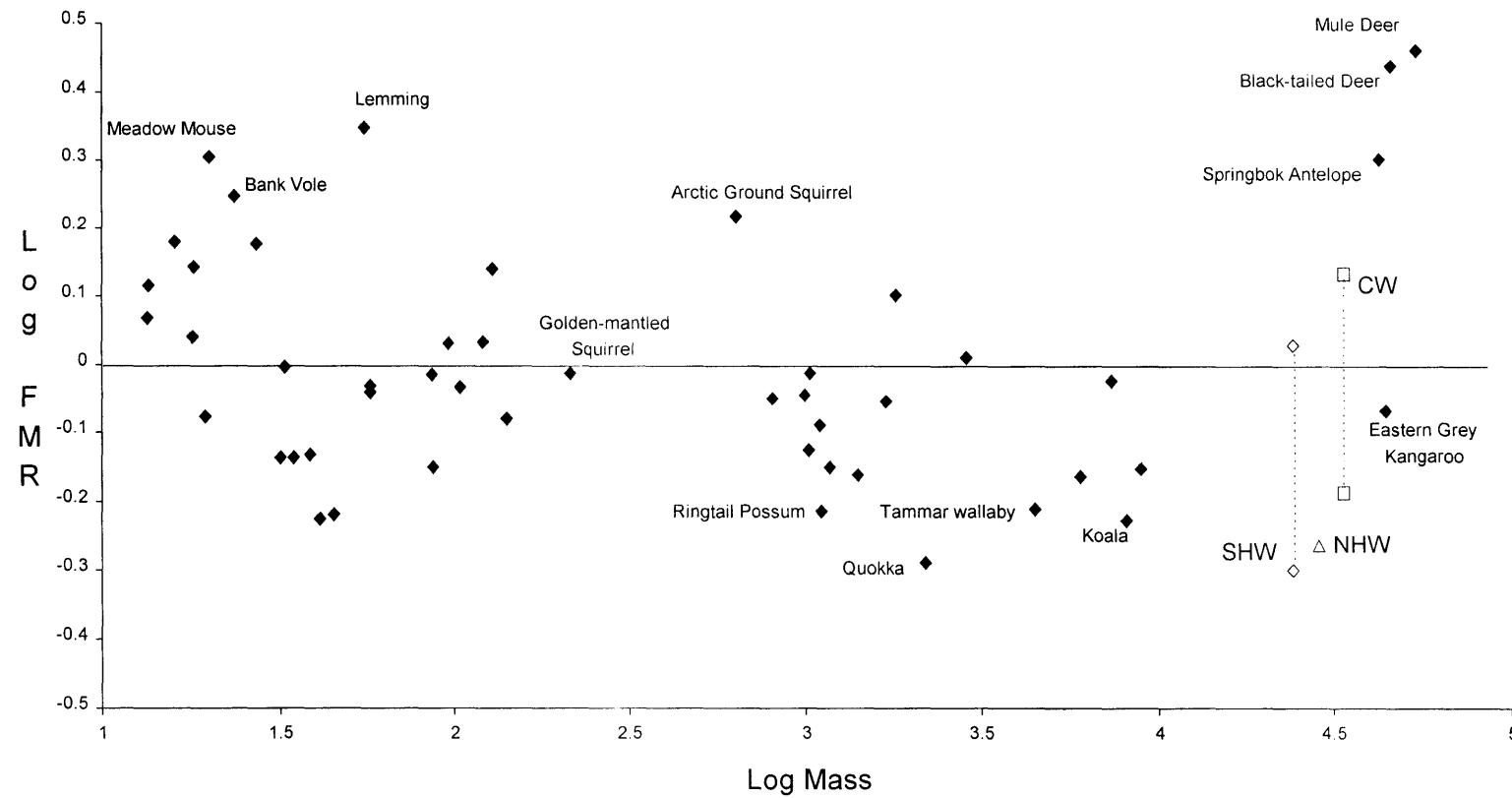


Figure 7.5 Field metabolic rates of herbivorous mammals. Values are residuals from a regression of FMR on body mass for 49 mammalian herbivores (names of some species are shown). The line represents the mean or 'expected' value for any body mass; only doubly-labelled water studies have been included. Seasonal values for wombats (open symbols) have been superimposed over the regression. For wombats: triangles = wet season, squares = dry season.

7.3.3 Feeding Rates

The rate of food intake necessary to provide the energy expended (FMR) by an animal can be calculated if the diet, energy content of the food and energy assimilation efficiency of the animal are all known. Fresh, green foliage typically contains about 21 kJ.g⁻¹ (dry matter) of gross chemical potential energy (Nagy 1983; Gipps and Sanson 1984; Nagy and Martin 1985) and fresh grass leaf contains about 15.9 kJ.g⁻¹ (dry matter) of gross chemical potential energy and grass seed contains about 16.2 kJ.g⁻¹ (dry matter) of gross chemical potential energy (Nagy *et al.* 1990). Gross chemical potential energy of grass leaf determined in this study was 16.3 kJ.g⁻¹ (dry matter) during summer and 16.0 kJ.g⁻¹ during spring and winter, and for grass seedhead was 16.6 kJ.g⁻¹ and grass sheath/stem was 14.8 kJ.g⁻¹ (Chapter 4). However, not all of this energy is able to be digested and metabolised by herbivores. The proportion of the total energy in food able to be utilised by a herbivore is known as the metabolisable energy which can be calculated if the energy assimilation efficiency is known. Energy assimilation efficiencies are often derived from the proportion of dry matter able to be digested in the diet. Barbosa and Hume (1992) found that wild common wombats had dry matter digestibilities of around 52% whereas southern hairy-nosed wombats had dry matter digestibilities of around 63%. Wells (1973) found southern hairy-nosed wombats in the laboratory had dry matter digestibilities of 60%. Calculations of the energy budgets need to take into account the energy lost through urine as urea and other chemicals, which for a herbivore is about 10% of the energy extracted from food (Nagy and Milton 1979; Hume 1982; Nagy and Martin 1985). These values for energy in food, energy assimilation efficiency and energy lost through urine are used in the following calculations of feeding rates.

Common wombat

Common wombats at mean body mass of 33.46 kg during the dry season required, on average, 5139 kJ.day⁻¹ from food to balance their energy expenditure in the

field. From dietary analyses (Chapter 4), common wombats at this time (summer '96) ate 45% leaf, 32% seedhead and 23% stem/sheath. Therefore, assuming the grass diet contains 16.05 kJ.g^{-1} dry matter (ie. $0.45 \times 16.3 + 0.32 \times 16.6 + 0.23 \times 14.8$), the metabolisable energy available to common wombats (with dry matter digestibilities of 52%) is $16.05 \times 0.52 = 8.35 \text{ kJ.g}^{-1}$, minus 10% lost through urine, leaving about 7.5 kJ net metabolisable energy per gram of dry matter ingested. The amount of food these animals must consume to maintain energy balance during the dry season is $5139 / 7.5 = 685 \text{ g.day}^{-1}$ of dry matter. During this period, grasses in their diet contained $71 \pm 6\%$ water (ie 29% dry matter) (Chapter 4). To maintain a dry matter intake of 685 g.day^{-1} , these wombats would have to ingest $685 / 0.29 = 2362 \text{ g.day}^{-1}$ of fresh grass. Mass changes were not significant for common wombats during the dry season and so I assumed that these animals were in energy and water balance.

Common wombats during the wet season required, on average, $10731 \text{ kJ.day}^{-1}$ from food to balance their energy expenditure in the field. Assuming 7.5 kJ.g⁻¹ metabolisable energy in grass (dry matter) is available to common wombats, these animals would need to have a dry matter intake of $10731 / 7.5 = 1431 \text{ g.day}^{-1}$ to balance energy expenditure during the wet season. During this period, grasses in the diet contained $60 \pm 8\%$ water (Chapter 4). To maintain a dry matter intake of 1431 g.day^{-1} , these wombats would have to ingest $1431 / 0.4 = 3578 \text{ g.day}^{-1}$ of fresh grass.

Southern hairy-nosed wombat

Southern hairy-nosed wombats during the dry season, on average, required 3142 kJ.day^{-1} from food to balance their energy expenditure in the field. Assuming their grass diet contains 16.0 kJ.g^{-1} (dry matter), the metabolisable energy available to southern hairy-nosed wombats (with dry matter digestibilities of 63%) is $16 \times 0.63 = 10.1 \text{ kJ.g}^{-1}$ leaving about 9 kJ net metabolisable energy per gram of dry matter ingested. The amount of food these animals must consume to maintain energy balance during the dry season is $3142 / 9 = 349 \text{ g.day}^{-1}$ of dry matter. During this period, grass contained $32 \pm 4\%$ water (Chapter 4). To maintain a dry matter intake of 349 g.day^{-1} , these wombats would have to ingest $349 / 0.68 = 513 \text{ g.day}^{-1}$ of fresh grass.

An alternative energy source to food is to catabolise fat reserves (fat yields 39 kJ.g⁻¹ metabolisable energy). Southern hairy-nosed wombats during isotope turnover periods in the dry season lost, on average, 94 g.day⁻¹ body mass. If this mass loss was all fat, the resultant energy yield of $94 \times 39 = 3666$ kJ.day⁻¹ is in the order of their estimated daily energy requirements (3142 kJ). Other sources of mass loss are excretion of faeces, urine and H₂O efflux.

Southern hairy-nosed wombats during the wet season, on average, required 6689 kJ.day⁻¹ from food to balance their energy expenditure in the field. Assuming 9 kJ.g⁻¹ metabolisable energy in grass (dry matter), these animals would need to have a dry matter intake of $6689 / 9 = 743$ g.day⁻¹ to balance energy expenditure during the wet season. During this period, grass contained 57 ± 7 % water (Chapter 4). To maintain a dry matter intake of 743 g.day⁻¹, these wombats would have to ingest $743 / 0.43 = 1728$ g.day⁻¹ of fresh grass.

Southern hairy-nosed wombats during wet season isotope turnover periods lost, on average, 84 g.day⁻¹ body mass. If the mass loss was all fat, the resultant energy yield of $84 \times 39 = 3276$ kJ.day⁻¹ is about half of their estimated daily energy requirements of 6689 kJ.

Northern hairy-nosed wombat

Northern hairy-nosed wombats during the dry season, on average, required 3802 kJ.day⁻¹ from food to balance their energy expenditure. I did not determine the energy assimilation efficiency of northern hairy-nosed wombats and so I have used the dry matter digestibility value determined by Barbosa and Hume (1992) of 63% for wild southern hairy-nosed wombats as an approximation to derive the metabolisable energy available to northern hairy-nosed wombats of 9 kJ.g⁻¹ dry matter. To maintain energy balance during the dry season, northern hairy-nosed wombats would require approximately $3802 / 9 = 422$ g.day⁻¹ of dry matter. The moisture content of grass at this time of year was not measured. In Chapter 6, I calculated the theoretical moisture content of grass (from water influx rates and FMR) to be 48%, which means that northern hairy-nosed wombats would require 819 g.day⁻¹ of fresh grass to maintain a dry matter intake of 422 g.day⁻¹. Since mass loss during the dry season energetics periods was not

significant (Chapter 6), I have assumed that northern hairy-nosed wombats were in energy and water balance.

7.4 DISCUSSION

7.4.1 Potential Errors

The doubly-labelled water method for measuring FMR involves a number of assumptions, which if violated could cause errors in estimates (Lifson and McClintock 1965). The assumptions which relate to total body water and water flux rates (used in calculations for FMR) are detailed in Chapter 6. In addition, there are a number of assumptions and potential errors that specifically relate to CO₂ production (a measure of FMR). These assumptions are that:

1. water and CO₂ flux rates are constant;
2. Isotopes label body H₂O and CO₂ only;
3. Isotopes leave body as H₂O and CO₂ only; and
4. No CO₂ input occurs via lungs or skin

Nagy (1980; 1989) evaluated the errors associated with these assumptions and states that estimates of CO₂ production are accurate to within 8%, based on laboratory validation studies of twelve species of mammals, three species of reptiles, seven species of bird and 4 species of arthropod. The doubly-labelled water method has since been further validated in humans (Klein *et al.* 1984), in a ruminant (Fancy *et al.* 1986), in another bird (Gales 1989) and in a folivorous marsupial (Nagy *et al.* 1990). Large errors in estimates have been found for animals that have evaporative water loss as a major component of total water efflux or that have high water flux rates compared to CO₂ production rates. Large errors have also been found in studies using arthropods, though the exact reason for this is not understood. These errors can be avoided by appropriate selection of study subjects (Nagy 1980).

A possible source of error in this study could be due to the violation of assumption number 4; no CO₂ input via lungs or skin. Errors arise if CO₂ enters the body

and this CO₂ is unlabelled or has a different concentration of labelled molecules to the body. Animals in confined and poorly ventilated areas, such as burrows, dens, enclosed nests etc. might be susceptible to violation of assumption number 4 because of possibly higher concentrations of exhaled CO₂ in the air. However, CO₂ exhaled from the study animal (doubly-labelled water) will not cause errors because the concentration of labelled molecules should be the same as in the body (Nagy 1980). Errors would be expected to arise in situations where gregarious animals communally inhabit enclosed spaces, and CO₂ inhaled by the study animal is derived from other animals.

The assumption of no CO₂ input (arising from unlabelled sources) via lungs whilst wombats were in burrows was not thought to apply in this study. Common wombats and northern hairy-nosed wombats are solitary and rarely share burrows (personal observations). Southern hairy-nosed wombats inhabited warrens within which a number of animals lived and which contained many closely spaced burrows. However, even within these warren systems, animals appeared to avoid sharing the same burrow (personal observations). I therefore assumed that errors due to violation of assumption 4 would be minimal for each of the wombat species.

Another possible source of error in estimates of FMR could be due to extra energy expended from carrying a radio-transmitter package. The generally accepted guide for adding extra weight to a study animal is not to exceed 5% of body mass for small animals and 1% for very large animals (MacDonald 1978), though this would depend on the species and type of study. The collars used in this study (incorporating a radio-transmitter and a data logger) weighed 300g, which is a small proportion (around 1%) of the total body mass of an adult wombat. Collars did not appear to irritate or impede the normal movements of animals observed in the field. I assumed that any effect the collars might have on normal behaviour or energy expenditure was insignificant.

Capture and Handling

This study aimed to investigate FMR of free-living wombats under natural conditions. As mentioned in Chapters five and six, human interference has the potential to affect natural (or ‘normal’) wombat behaviour (and hence alter FMR). In any study

that assumes natural behaviour of study individuals, unquantified deviations in measurements resulting from human interference are a source of potential error.

If wombat behaviour was indeed disrupted and resulted in higher than normal FMR (from increased activity as suggested in Chapter five), the significance for this study will be for more conservative results. In other words, for these species with inherently low FMR, disrupted behaviour may result in normal WTR being even lower than that measured.

7.4.2 Energy Metabolism

Field metabolic rates of wombats during the wet season were above the ‘mean’ field metabolic rate for mammalian herbivores that I calculated from the literature, whereas dry season FMR’s were well below this mean. Most studies of FMR in herbivorous mammals have been conducted on small (< 100 g) animals; the only species above 10 kg (excluding humans and domestic animals) for which data on FMR are available are springbok antelope *Antidorcas marsupialis* (42 kg, n = 4) (Nagy 1987; 1994b), eastern grey kangaroo *Macropus giganteus*, (44 kg, n = 2), black-tailed deer *Odocoileus hemionus columbianus* (48 kg, n = 5) (Nagy *et al.* 1990) and mule deer *Odocoileus hemionus* (54 kg, n = 2) (Nagy 1987). Data for the eastern grey kangaroo and black-tailed deer come from the dry season, the dates of the studies of the other two species are not specified in the literature. Field metabolic rates for each of the wombat species during the dry season were less than that of an eastern grey kangaroo during the same season, with the rate for the two hairy-nosed species being less than half of that for an eastern grey kangaroo. Field metabolic rate of southern hairy-nosed wombats during the dry season was only 17% of that of the similarly-sized springbok during the dry season. The field metabolic rate of common wombats during the dry season was also less than that of an grey kangaroo during the same season, and only 27% of that of a springbok.

The seasonal patterns of field metabolic rates were remarkably similar for the three wombat species. This is despite major climatic differences between the habitats

and the fact that they belong to two different genera. FMR varied markedly between seasons, with rates during the wet season being about double those of the dry season. The fact that southern hairy-nosed wombats and common wombats demonstrated similarly large differences in seasonal FMR is interesting given the different seasonal factors affecting each species. During the dry hot summer, southern hairy-nosed wombats face a lack of drinking water and their dry food is of poor nutritional quality and probably of low availability. Rainfall during the cooler winter is still low, but sufficient to maintain pasture growth. Common wombats during the dry winter do not face low availability of either water or food, though low temperatures (often resulting in snow and heavy frosts) reduce pasture growth. During this period ‘poor’ quality species increase their dominion of the pasture. Thus, for southern hairy-nosed wombats the wet season is more favourable in terms of increased food quality, quantity and water availability, whereas for common wombats the wet season is more favourable in terms of food quality.

Wombats were able to maintain body mass and condition in both the dry and wet seasons, suggesting that the reduced energy expenditure during the dry (poor) season was effective in maintaining energy balance. The ability of southern hairy-nosed wombats to maintain condition during poor seasons was also noted by Gaughwin *et al.* (1984), who found that southern hairy-nosed wombats were able to withstand severe drought combined with shortage of feed due to sheep grazing without drastic changes in condition (as indicated by fat reserves and haematological data).

Field metabolic rates of southern hairy-nosed wombats during the dry season were 2.0 times the basal metabolic rate of $1577 \text{ kJ}.\text{day}^{-1}$ for this species as determined by Wells (1978). The wet season FMR was over four times this basal metabolic rate. Barboza (1993) found no significant differences between the basal metabolic rates of southern hairy-nosed wombats and common wombats, and the mean value of $1704 \text{ kJ}.\text{day}^{-1}$ is similar to that obtained by Wells (1978) for southern hairy-nosed wombats. Seasonal FMR’s of common wombats were 3.1 and 6.3 times the BMR values obtained by Barboza (1993), in the dry and wet seasons respectively.

Field metabolic rates are expensive to measure, and so simple multiples of BMR have been widely used as an index of FMR. For example, FMR has been expressed as 2

times BMR in small mammals (Golly 1960) and 2 to 3 times BMR for mammals in general (Karasov 1981; Robbins 1983). However, the FMR:BMR ratio has been found to vary according to factors such as taxon and body mass, with ranges as large as from 1.5 to 5.0 (Degen and Kam 1995), and more recent studies suggest that ratios as large as 6 are not unusual (K. Nagy, pers comm, Hammond and Diamond 1997). The large interseasonal variation in the FMR:BMR ratio in wombats suggests that using simple multiples of BMR as an index of FMR is inappropriate because seasonal effects on FMR can be profound.

7.4.3 Feeding Rates

Common wombats had higher estimated feeding rates than the hairy-nosed species during each season. During the dry season, common wombats were estimated to eat around 2.0 kg of fresh grass per day, whereas estimated feeding rates of southern hairy-nosed wombats and northern hairy-nosed wombats were about 25% of this value. During the wet season, the estimated feeding rate of southern hairy-nosed wombats was about 56% of that estimated for common wombats. Differences in estimated feeding rate were due to a combination of factors, including differences in moisture content of food and differences between the species in body mass, energy requirements and apparent dry matter digestibilities. The marked difference in feeding rates between common wombats and southern hairy-nosed wombats during the dry season was mostly due to the large difference in moisture content of food, with common wombats ingesting grass that contained about twice as much free water as that eaten by southern hairy-nosed wombats (74% compared to 32%).

The estimated dry matter intake of southern hairy-nosed wombats during summer in this study ($262 \text{ g}.\text{day}^{-1}$) is similar to the $201 \text{ g}.\text{day}^{-1}$ estimated by Wells (1973) based on water turnover rate and the moisture content of grass. No data are available from previous studies for feeding rates in the field of northern hairy-nosed wombats or common wombats. Estimated feeding rates of all species of wombat were well below that predicted from the generalised equation of Nagy (1987) for feeding rates (dry matter intake) of marsupial herbivores:

$$\text{DMI g}.\text{day}^{-1} = 2.09 \text{ Mass}^{0.68}$$

This equation is based on FMR and metabolisable energy in food. The estimated feeding rate of common wombats during the wet season was 43% of the predicted value, while the dry season feeding rate was 21% of the predicted value. Southern hairy-nosed wombat feeding rates during the wet and dry seasons were 28% and 13% respectively, of the rate predicted for a 24 kg marsupial herbivore. The feeding rate for northern hairy-nosed wombats during the dry season was 14% of the predicted rate. These low feeding rates are consistent with the results obtained by Barboza *et al.* (1993) which demonstrate low nitrogen requirements and low dry matter intake of common wombats and southern hairy-nosed wombats in the laboratory.

7.4.4 Summary

Field metabolic rates were similar between wombat species, and were highly seasonal, with wet season rates approximately double those of dry seasons. Field metabolic rates during the wet season were slightly above the marsupial ‘mean’ whereas dry season FMR’s were well below the mean and, for the southern hairy-nosed wombat, are amongst the lowest recorded for herbivorous mammals. Feeding rates were well below values predicted for herbivorous marsupials; they also varied markedly between the species and were highly seasonal. Wombats were able to maintain condition during the dry season (Chapter 6), suggesting that by ‘switching off’ (reducing energy expenditure) during the dry (poor) season, they were still able to maintain energy balance.

CHAPTER 8

SYNTHESIS AND GENERAL

DISCUSSION

8.1 INTRODUCTION

This study is the first to investigate the energetics (field metabolic rates) of free-living wombats, and the first to examine water turnover rates in the field for two of the three species. It is also one of few studies (excluding studies of *Homo sapiens*) to have investigated the field energetics of medium to large sized mammals. Prior to this study, of the four herbivorous mammal species greater than 10 kg for which data on FMR (using comparable doubly-labelled water methods) were available, only one was a marsupial (eastern grey kangaroo). This study has provided information on FMR and WTR for a further three large (30-40 kg) species of marsupial from two genera.

The aim of this study was to examine the thesis of conservative energy expenditure amongst the Vombatidae by investigating the ecological energetics and nutritional ecology of free-living wombats (Chapter 1). The seminal observations for this thesis were 1) that wombats are able to exist in seasonal or intermittently productive environments in which the quality or quantity of food and the availability of water may fluctuate strongly (Chapter 2), and 2) that the species possess characteristics indicative of the energy-conservative extreme of this energetics continuum. In Chapter 1, I proposed that the Vombatidae coped with fluctuations in food resource quality/quantity and water

availability by using a collection of adaptations or strategies that were unique amongst mammalian herbivores and which comprised an adaptive syndrome for energy conservation.

I divided the thesis into the examination of a number of hypotheses or factual expectations, which were organised into four chapters (4 to 7) with the broad headings of Food Resources and Feeding Ecology, Home-range and Activity, Water Turnover, and Energetics. The foraging environment of wombats was assessed in Chapter 4 in terms of food availability and nutritional quality. This provided the seasonal backdrop against which wombat physiological and behavioural responses could be viewed, and hence strategies evaluated. I also analysed diets and feeding selectivity in Chapter 4 to examine digestive and feeding strategies. In Chapter 5, I investigated the responses of wombats to changes in food quality or availability in terms of home-range use, habitat use, activity levels and the size and location of the home-range. Rates of water turnover and metabolism in the field, two fundamental aspects of the thesis, were examined in Chapters 6 and 7. From these measures I was able to infer the extent of minimisation of energy expenditure in the Vombatidae. The first two chapters provided background on theoretical aspects of ecological energetics, digestive and feeding strategies, and evolution and ecology of the Vombatidae. Chapter 3 presented an overview of the plan and methodology of the study. In this final chapter, I summarise and synthesise the findings from the different chapters in order to draw conclusions on the ecological energetics of the Vombatidae and the proposed adaptive syndrome. Firstly, I consider the ‘bottom line’ of the thesis; are wombats energy conservers? I then place ‘wombatism’ in the context of the grazing marsupials by comparing the Vombatids to the other group of marsupial grazers, the Macropodids. From this I draw conclusions about evolutionary strategies for marsupial grazing. I discuss and summarise Vombatid strategies for coping in a fluctuating environment, and implications for management. I conclude by considering the hypothesised adaptive syndrome proposed in the introductory chapter.

The data for common wombats were collected from a site that is reasonably typical (from qualitative observations) for this species in terms of habitat and climate (that is, habitats that are cool, forested, mountainous and mesic). However, the range of

habitats occupied by this species is far broader, and includes alpine areas, coastal heath and dryer sclerophyll habitats. Therefore, the results for common wombats in this study may not extrapolate to other areas within the species' distribution. This caveat also applies to the results for southern hairy-nosed wombats.

8.2 ARE WOMBATS 'ENERGY CONSERVERS'?

As outlined in Chapter 1, from an energetics viewpoint mammals occupy a continuum that ranges from species having maximal energy intakes (with correspondingly high mass-specific rates of metabolism, growth, reproduction and activity) to species having minimal energy expenditures (low mass-specific rates of energy intake combined with physiological and behavioural adaptations to minimise daily energy expenditure). This study has shown (Chapters 6 and 7) that all three species of wombat have seasonally low field metabolic rates and, for the arid-adapted *Lasiorhinus*, exceptionally low water turnover rates. Interestingly, FMR for both *Vombatus* and *Lasiorhinus* showed a similar and marked response to changes in seasonal conditions, despite the striking differences between their habitats and range climates (mesic vs semi-arid). FMR during the 'good' season for either genus was not substantially different from that expected for an average mammal of their body size (indeed, FMR was slightly higher than expected). FMR for the poor season, however, was about half of that during the good season and, for *Lasiorhinus* spp., was amongst the lowest recorded for mammals. The similarity in FMR and its seasonal responses between the genera suggest that FMR is not driven by the thermal environment.

Whereas seasonal fluctuations in FMR appear to be independent of habitat or climate and thus an intrinsic adaptation of the Vombatidae, WTR largely reflected habitat/climatic differences and varied significantly between the genera. WTR for the mesic-adapted *Vombatus* was above the marsupial 'mean' and did not show substantial seasonal variation. WTR for *Lasiorhinus* during the 'good' season was slightly below the marsupial mean, whereas WTR during the 'poor' season was amongst the lowest recorded for mammals (and was more aligned with those of reptiles). The relatively large (and in some cases extreme) deviations in FMR and WTR from that expected for their body size, and the direction of these deviations, supports the hypothesis that wombats are

‘energy conservers’, lying close to the energy ‘minimiser’ extreme of the maximiser-minimiser continuum. Such an energetically frugal existence contrasts to that of other marsupial grazers; and their differences and adaptive significances are compared in the following section.

8.3 VOMBATIDS AND MACROPODIDS: THE MARSUPIAL GRAZERS

8.3.1 Overview

The extant native grazing mammals of Australia are represented by the Vombatidae and the Macropodidae. The larger species of Macropodidae (such as the red kangaroo, eastern grey kangaroo and western grey kangaroo) show similarities to wombats in body-size, diet and habitat. For example, adult female eastern grey kangaroos weigh up to 35 kg, though males may attain three times that weight (Peter Jarman pers comm), and adult common wombats in this study ranged from 20 to 39 kg. Eastern grey kangaroos are grass specialists, with greater than 95% of the diet being grasses (Jarman and Phillips 1989). Wombats are also grass specialists; the diet of common wombats in this study comprised 95% grass. Eastern grey kangaroos are sympatric with both common wombats and northern hairy-nosed wombats (Poole 1995; McIlroy 1995; Johnson and Gordon 1995) and, within their overlapping distributions, also occur in the same habitats (pers obs). During this study, I observed eastern grey kangaroos at the Epping Forest and Riamukka study sites, and at the latter site at least, foraging ranges of both species overlapped. The diets of eastern grey kangaroos overlapped by greater than 90% with those of northern hairy-nosed wombats at the Epping Forest site (Woolnough 1998) and with those of common wombats at the Riamukka site (Jeffery 1996). Despite similarities in body size, diet and habitat between the two families of marsupial grazers, they differ markedly in many other aspects of their ecology, such as metabolic rate, water requirements, burrowing, ranging and foraging behaviour, sociality, digestive physiology and reproductive rate. These differences (discussed in greater detail below) suggest that Macropodids and Vombatids have evolved very different strategies as mammalian grazers.

8.3.2 Field Metabolic Rate and Water Turnover Rate

Vombatids and Macropodids differ in their rates of metabolism and water turnover (Chapters 6 and 7). This study has shown that seasonal FMR for wombats can fall much lower than that expected for a similar-sized marsupial (or eutherian) herbivore. The only Macropodid grazer (and marsupial of similar size to a wombat) for which FMR data is available is the eastern grey kangaroo, and this data was obtained during the dry (poor) season (Nagy *et al.* 1990). Field metabolic rates for each of the wombat species during the dry season were less than that of an eastern grey kangaroo, with the rate for the two hairy-nosed species being less than half of that for an eastern grey kangaroo (Chapter 7).

Low FMR not only affects energy requirements and thus food requirements, it influences water requirements. Low FMR enables low WTR, though observed WTR for individuals are more often a reflection of the water content of food and the use of water for evaporative cooling. This was illustrated in Chapter 6 by the large variations in WTR in wombats between habitats and seasons. Common wombats and eastern grey kangaroos inhabit mesic environments, and a large proportion (if not all) of their water requirements can be met from water contained in their food. The similarity in water turnover rates between the two species (Chapter 6) is not surprising given the similarity in their grass diets, both of which have a high water content. Water turnover rates of the arid-adapted hairy-nosed wombat species during the dry season were low. In fact, WTR for southern hairy-nosed wombats during the dry season were only 39% of that predicted for a similarly-sized macropodid during the same season. Mass-specific WTR for southern hairy-nosed wombats was only about a third of that for either a red kangaroo or a euro *Macropus robustus erubescens* (Dawson *et al.* 1975) (both macropodid species are arid-adapted). The arid-adapted wombats exist in areas where free surface water may not be available for weeks or even months. Low FMR (Chapter 7) combined with the use of burrows (and consequent reduction in water loss), ability to produce a moderately concentrated urine and faecal pellets of low moisture content (Wells 1973) are likely to explain the extremely low water requirements of the arid-adapted hairy-nosed wombats. Low energy requirements combined with low water requirements mean that wombats should be able to utilise low quality foods that are also dry. This may explain the ability

of southern hairy-nosed wombats to survive on forage of lower water content than can other grazing mammals. Southern hairy-nosed wombats in this study were apparently able to obtain almost all of their water requirements (some water possibly derived from catabolism of fat) during the dry hot summer from forage that contained as little as 32% moisture, whereas other mammalian herbivores have been known to cease feeding (in the absence of drinking water) when moisture content falls below about 50% (Chapter 6). In contrast, red kangaroos and euros probably need to drink regularly in arid areas. This is suggested by the common observation in arid areas of red kangaroos regularly drinking at dams and water holes, the large distances travelled by red kangaroos to water sources (especially during dry periods), the sometimes high mortality of red kangaroos and wallaroos during drought, and their requirement of a green grass diet for reproduction (Newsome 1995).

8.3.3 Burrowing vs non-burrowing

One of the most obvious differences between Vombatids and Macropodids is in fossoriality. Wombats are obligate users of self-dug burrows whereas kangaroos do not use burrows. As detailed in Chapter 1, burrows are clearly an integral part of wombat ecology; they spend as much as 70% of their lives in their burrows (McIlroy 1973; Wells 1973; pers. obs) emerging when outside conditions (such as temperature and humidity) are favourable (Johnson 1991a). Individuals have been known to die during the day in summer when access to burrows has been denied through trapping (McIlroy 1973; A. Horsup pers comm.) (though wombats in captivity can survive without burrows under suitable conditions). The use of a burrow can confer advantages on a homoeotherm by reducing thermoregulatory costs; this may be through minimising exposure to temperature extremes or by providing a relatively thermoneutral environment. In arid environments, the use of burrows can be important in reducing water loss by reducing the need for evaporative cooling and by maintaining higher humidity levels in the burrow than outside thereby reducing water loss across body surfaces (eg. Bradley and Yousef 1972; Nagy and Gruchacz 1994). A burrow also provides a safe refuge from predators, allowing long periods of relative inactivity without the costs of vigilance and predator evasion. Wombats appear to spend most of their time in burrows sleeping or otherwise

relatively inactive (Triggs 1996, Chapter 5). Fossoriality, therefore, probably plays a key role in enabling wombats to achieve low FMR and WTR.

Recently, Johnson (1998) reviewed the adaptive significance of burrow-use, diet and body-size, in an attempt to explain the anomalous burrow-use amongst the Vombatidae. Most small mammals use burrows, and this is not surprising given that no specialised digging adaptations are necessary and substantial benefits are likely to be realised in terms of predator protection and thermoregulation (large body surface area to volume ratio). Small mammals are also able to spend a large proportion of their time in the burrow because they feed on food concentrated in energy which reduces foraging time. At the other end of the scale, there is undoubtably an inherent limit on body-size and burrowing, simply due to engineering constraints (depth of soil profiles and stability of tunnel structures). However, the incidence of burrowing sharply declines as body mass exceeds about 10 kg, well below the expected largest possible size. Compared to small herbivores, large herbivore can eat poor quality foods and to sustain their larger absolute energy requirements large herbivores tend to forage for long periods which leaves little time to spend in a burrow. For larger herbivores, burrowing is likely to be more energetically expensive, as burrow volume (and hence volume of material that must be dug out) increases as the cube of body length/width, whereas bone and muscle strength increase as the square of linear dimensions. Johnson (1998) suggests that for animals greater than about 5 or 10 kg, the (increased) costs of burrowing outweigh the limited time able to be spent in the burrow realising the advantages.

8.3.4 Ranging and foraging behaviour

Wombats and the grazing macropods differ markedly in the size and use of home ranges, in distances travelled and in foraging behaviour. Common wombats and northern hairy-nosed wombats do not range far from their burrows, and return to burrows before dawn (Johnson 1991a; this study). The conservative home-ranges of common wombats in this study (7 to 32 ha) are similar to those reported in other studies of common wombats (5 to 23 ha, McIlroy 1973; 8 to 13 ha, Taylor 1993) and northern hairy-nosed wombats (27 ha, Johnson 1991a; 31 ha, Woolnough 1998). These species also show high fidelity to a set of burrows (pers obs) and, except for dispersing sub-adults (and

perhaps adult females of the northern hairy-nosed wombat, Johnson 1991a), rarely move to another area and another set of burrows. Thus home-ranges of common wombats and northern hairy-nosed wombats (and presumably southern hairy-nosed wombats), are conservative in size and wombats show high fidelity to them (Johnson 1991a; this study). Common wombats in this study showed remarkably little seasonal variation in the size, shape or location of home-ranges or of the location of feeding areas. Ranging behaviour for common wombats (and thus most likely foraging behaviour) also showed little variation between seasons, though there was some evidence that they spent more time outside burrows during winter (the poor season). Conservative foraging behaviour in wombats might be partly due to the possible benefits of maintaining short-grazed 'lawns', as discussed in the next section.

In contrast to the Vombatidae, the size and location of home-ranges of kangaroos are not constrained by the requirement to return each day to a fixed location (such as a burrow). Kangaroos range more widely than do wombats, and locations and sizes of home-ranges may change seasonally or yearly. For example, home-ranges of eastern grey kangaroos in New South Wales varied from 30 to 90 ha in one study (Peter Jarman pers comm), and have been reported as large as 300 ha in another study (Jaremovic and Croft 1987). Eastern grey kangaroos have been shown to vary their ranging distances and daily foraging time strongly with seasons. Clarke *et al.* (1989) found that eastern grey kangaroos moved further and faster in summer than in winter, and spent more time selecting food items and feeding in winter than in summer. Eastern grey kangaroos have been shown to change foraging sites in response to fire (which promotes green grass shoots) or seasonal changes in vegetation, and their distribution within the home range during feeding can be explained in terms of pasture greenness (and other factors) (Hill 1982; Southwell 1987). Eastern grey kangaroos at the Epping Forest site moved off the Reserve to adjacent grazed properties during periods of good rainfall, returning as conditions became drier (Woolnough 1998).

8.3.5 Feeding strategies and digestive physiology

Vombatids differ from Macropodids and large hindgut fermenters in the time spent foraging. Eastern grey kangaroos have been shown to spend between 10 and 18 hrs

per day feeding (Southwell 1981; Clarke *et al.* 1989). These times are comparable to those of large hindgut fermenters such as equids, which have been reported to feed around 15 hrs per day (Duncan *et al.* 1990). Common wombats in this study spent around 2 to 8 hours above-ground, which is similar to the results obtained for common wombats (3 to 8 hrs) by McIlroy (1973) and for northern hairy-nosed wombats (2 to 6 hs) by Johnson (1991a). However, opportunistic observations and radio-tracking data in this study have shown that not all of the time wombats are above-ground is spent feeding, and this is supported by the results of other workers (McIlroy 1973; Johnson 1991b; Woolnough 1998; Alan Horsup pers comm). Wombats spend time ranging, visiting and maintaining burrows, and presumably socialising to some limited extent. In addition, wombats also spend substantial periods (up to an hour) sitting at the entrance of the burrow following emergence, before moving away from the burrow.

Wombats are conservative in their ranging and foraging behaviour, using well worn paths to feeding areas. Feeding areas appear to be used habitually, and may be intensively grazed (pers. obs) to become ‘lawns’ or grazing haloes (if around burrows). Opportunistic observations of wild and captive wombats suggest that they tend to pluck grass rapidly while staying in the same place, rather than the bite-and-move behaviour of sheep and kangaroos. It is possible that wombats cannot afford much time searching for food items, and that this partly explains the use of well worn trails to habitually used feeding sites and the non-searching style of feeding pattern. Maintenance of short grass might also maximise the ‘plucking’ efficiency of the opposed incisors of wombats, allowing them to graze closer to the ground than macropodids of similar body mass. Thus, using the same feeding areas for all seasons might be of more benefit to wombats than switching areas.

Vombatids and Macropodids differ in their digestive physiology (Chapter 2), despite both marsupial families being grazers. Vombatids extract energy from food fibre using the hindgut fermentation strategy as do many very large grazing or browsing eutherian herbivores such as equids and elephants, and many small herbivores such as rodents. This digestive strategy contrasts to the foregut fermentation strategy used by all other grazing marsupials (Macropodids) and eutherians such as ruminants (deer, cattle, sheep, goats etc.). As outlined in the first two chapters, the hindgut fermentation strategy

is suited to maximising the efficiency of energy extraction from soluble carbohydrate rather than from structural carbohydrate (fibre) whereas the foregut fermentation strategy is suited to maximising extraction of energy from fibre. The ‘tubiform’ foregut fermenters (Macropodids) and the hindgut fermenters apparently both have lower digestive efficiencies than the ruminants, but compensate by having higher rates of food intake (cf. Janis 1976; Hume 1982; Owen-Smith 1988). The ruminant foregut strategy might have evolved in response to (intermittent) constraints in food abundance, since they are able to subsist on less food (Janis 1976).

The Macropodid foregut fermentation system and the Vombatid hindgut fermentation system have reported similar levels of fibre digestibility on high fibre diets (Freudenberger and Hume 1992). Wombats have also achieved fibre digestibilities comparable to those of much larger hindgut-fermenters such as zebra and tapir on high fibre diets (Foose 1982, cited in Barboza 1993). The greater-than-expected (for body size) fibre digestibility of Vombatids has been attributed to the slower rate of digesta passage and greater-than-expected gut volume (Barboza 1993). However, despite wombats achieving similar levels of fibre digestibility to those of larger grazing mammals, their lower rate of food intake means a lower rate of energy absorption. Undoubtedly, lower mass-specific energy requirements from food and efficient energy extraction from cell contents enables wombats to accept lower rates of absorption associated with delayed digesta passage, in order to achieve more complete fermentation of fibre. A strategy of delayed digesta passage to allow more complete digestion is suited to an animal that spends most of its time resting in burrows rather than foraging and hence has a low rate of food intake. This strategy also enables wombats to subsist on less food, that can be found close to the burrow.

A feeding strategy theoretically open to wombats and other hindgut fermenters is to exploit the ‘duplex’ nature of some food resources (Chapter 1). This strategy involves having a high intake of food resources consisting of a mix of easily digested soluble carbohydrates, easily fermented structural carbohydrates and less digestible fibre (a mix found in leaf and stem). Energy and nutrients are extracted from the fractions that are easily digested and easily fermented, and the remaining fibre is passed through the system to make room for more material. This seems to be the strategy adopted by

grazing equids and very large browsers such as elephants, and small body-size caecal-fermenters such as lagomorphs and certain rodents (Owen-Smith 1988). For large herbivores that feed on food dilute in energy, such a strategy would appear to depend on a high rate of food intake. Their low rate of food intake suggests that the Vombatids are not exploiting the ‘duplex’ nature of food resources to the extent of the larger hindgut fermenters.

Wombats appear to use a strategy of low intake combined with maximising the breakdown of food by mastication to increase digestive efficiency. Maximising cell breakdown by mastication is suggested by the continuously growing molars and premolars, molarform premolars, narrow palate and strong jaw muscles in wombats which indicate a powerful dental mill. This strategy would have a number of advantages for a wombat-sized hindgut fermenter. Wombats have a smaller fermentative capacity (and hence shorter fermentation times and/or lower rate of intake) than larger hindgut fermenters (such as equids) and so are likely to break down a lower proportion of cell walls by fermentation, releasing a lower proportion of cell contents into the digestive tract. Increased cell rupture (and therefore increased release of cell contents) by mastication should help compensate for the lower proportion of cell walls ruptured by fermentation in wombat digestive tracts. Increased cell rupture by mastication also means that a greater proportion of the cell contents are made available to the foregut gastric system rather than being released into the hindgut during fermentation. Energy from soluble carbohydrate is extracted more efficiently by the grazer if cell contents are released into the foregut (gastric digestion) than if they are released into the hindgut (microbial fermentation) (outlined in Chapter 1). Increased mastication produces smaller particle size and hence greater surface area upon which digestive processes can act. Food particles obtained from stomachs and faeces of southern hairy-nosed wombats have been found to be ground to a smaller size than those obtained from red kangaroos and grey kangaroos (Dierenfeld 1984, in Wells 1989). Thus, the strategy of using a combination of powerful dental mill and foregut gastric digestion is suited to the efficient extraction of energy from cell contents, and smaller particle size of digesta and slow digesta passage assists extensive fermentation of fibre.

As discussed in the first two chapters, reasons why Vombatids and Macropodids have evolved different fermentation strategies is unclear (given that they can obtain similar levels of fibre digestibility) and is probably due to the trade-off between maximising the efficiency of energy extraction from food (hindgut fermentation) versus access to vitamins synthesised by gut microbes (foregut fermentation) (for example, Janis 1976; Demment and Van Soest 1985; Owen-Smith 1988). 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. Large body-size facilitates extraction of energy from fibre due to large gut volumes and inherently longer fermentation times, and this confers advantages in terms of utilising abundant but poor quality food resources. Why the marsupial grazers (wombats and macropods) have not increased body size for this reason is uncertain. On continents other than Australia, body masses of eutherian herbivores cover the 20 to 40 kg range (as do wombats) in numerous species, but the largest body masses are an order of magnitude greater (ie. 100 to 1000 kg) than the extant Australian marsupial herbivores. Macropodids have not (either in the present or in the past) evolved very large body sizes (probably only to around 200 kg), and possibly an inherent size limit exists to the hopping form of locomotion. Vombatid forms with large body mass (probably 250 kg plus) existed in the past (Murray 1998), but reasons for their demise may have been due to human predation rather than related to food resource constraints.

8.3.6 Sociality

The social system of the eastern grey kangaroo contrasts strongly to that of common wombats. Eastern grey kangaroos are gregarious, living in matrilineal groups that may number twenty or more. Common wombats appear to be solitary; with the exception of mothers and their young, individuals feed alone, seldom directly interact and rarely share burrows. Reasons why sociality has developed amongst some groups of mammals, such as the large grazers, have been put forward by Bell (1970), Jarman (1974) and others, and involve relationships between metabolic rate, body size, diet,

dispersion of food resources and predator avoidance. The development of sociality amongst the larger grazing macropodids may be partly related to predator avoidance through increased vigilance and numbers of individuals. Spending most of their time inactive in burrows, wombats probably have little time for complex socialising or home-range defence. Other burrowing mammals have developed complex social systems, but they tend to be (diurnally) active (ground squirrels, rabbits) or carnivores (cooperative hunters). Wombats use scent marking (faeces and urine) as social signals to other individuals. This method of communication is less time-consuming and less energetically expensive than ranging in order to meet and check all individuals within the range.

8.3.7 Reproductive rate

Reproductive rates of the Macropodidae are higher than those of the Vombatidae. For example, during good conditions eastern grey kangaroos may produce just over one young per year, and at any one time a female may have a young-at-foot and a pouch-young both suckling, with a ‘paused’ blastocyst ready to continue development once the pouch-young has vacated the pouch. Female common wombats do not produce overlapping young as do eastern grey kangaroos. Young common wombats reach weaning age at around 15 or 16 mths (Triggs 1996), after which time the pouch is again suitable for a newly born young. Thus common wombats probably produce one young about every 1.5 years during normal seasonal conditions. There is some evidence that southern hairy-nosed wombats require three consecutive years of good rainfall for breeding and survival of young, and hence recruitment to the population (Wells 1995). This might also be true of northern-hairy nosed wombats, given their low recruitment rate to the population (Alan Horsup pers comm). Reproduction is energetically expensive and low rates of reproduction are consistant with low rates of energy expenditure.

8.4 VOMBATIDS AND MACROPODIDS: TWO STRATEGIES FOR MARSUPIAL GRAZERS?

Overall, a picture emerges of two major groups of marsupial having evolved different strategies for grazing. The Macropodids are social, non-burrowing, free-

ranging, foregut fermenters with high (compared to wombats) rates of food intake and reproduction. The Vombatids contrast by being fossorial, conservatively ranging, hindgut fermenters with seasonally low rates of metabolism and water turnover, and low rates of food intake and reproduction. Fundamental to the different strategies is the difference in energetics and its effect on energy and nutritional requirements from food. The Macropodids represent the more ‘conventional’ strategy for mammalian grazing, whereas the Vombatids represent an energetically conservative strategy. These two strategies are summarised below.

Compared to Vombatids, Macropodids most likely meet their higher energy requirements through selection for higher quality food resources, and possibly through higher rates of food intake. Greater feeding selectivity by kangaroos is also suggested by the narrow ‘deer-like’ facial morphology (suited to selection of food items from amongst the grass sward) compared to the broad cow-like muzzle of wombats. There is some evidence that eastern grey kangaroos at Riamukka ate a higher proportion of ‘good quality’ grasses than wombats did (Jeffery 1996). The larger grazing Macropodids are mobile and able to forage over large areas in search of higher quality items or move to new feeding areas if necessary. Ranging patterns and locations of feeding areas are flexible and responsive to changes in the foraging environment. The foregut fermentation system of Macropodids is suited to extracting energy from fibre and also enables them to take advantage of nutrients synthesised by gut microbes. The tubiform stomach (as opposed to the ruminant stomach modification) is suited to high rates of intake. Despite the requirement of Macropodids for regular drinking in arid environments (low food moisture content and high ambient temperature), their mobility allows them to forage away from permanent water, to move between widely spaced water sources and to follow localised rainfall events (a source of free surface water or green pick).

In contrast to the ‘conventional’ and mobile Macropodids, the more sedentary Vombatids live an energetically frugal lifestyle. Wombats have been able to achieve exceptionally low FMR and WTR through fossoriality (via reduced costs of thermoregulation, vigilance and predator avoidance), low BMR, low activity and low rates of growth and reproduction. Burrow use is clearly a key factor in reducing energy

expenditure for wombats, but the obligate use of burrows also restricts their ranging and prevents populations shifting to other areas where food resources might be seasonally or ephemerally of better quality. Thus, the energy requirements of a wombat during all seasons must be satisfied from food resources close to its burrows. Their potentially low FMR (partly as a result of using burrows) enables them to do this by reducing the requirement for food concentrated in energy. When eating food high in fibre concentration and dilute in easily digestible cell-contents, wombats delay digesta passage to obtain fermentation rates comparable to larger herbivores. Because wombats do not range over large areas or need to be rapidly mobile for long distances they are able to have a large voluminous gut relative to their body-size (Barboza and Hume 1992). A large gut and slow passage rate of digesta allows greater retention time and hence more complete digestion (Barboza 1993). Their digestive strategies, combined with low energy requirements from food, may allow wombats to accept forage of lower quality, which can be gathered less selectively and against lower interspecific competition, enabling wombats to spend less time foraging and more time inactive while food is digesting. Such adaptations appear to enable wombats to use the poorer quality pasture components as a dietary staple, but also take advantage of the relatively good pasture components when available. The low absolute energy requirements of wombats might be advantageous under conditions of low forage abundance, such as drought. Unlike the Macropodids, wombats are not able to travel large distances to water sources, and therefore the availability of water to wombats is determined by the water content of food and the presence or absence of free surface water close to burrows. It is possible that common wombats use burrows closer to water during drier periods, though this has not been investigated. The use of burrows and other adaptations to reduce FMR and WTR, however, has freed wombats of the need to regularly drink (at least during ‘normal’ years), enabling them to survive in semi-arid areas lacking permanent surface water, and to use the dry, poor quality forage in these areas.

Differing requirements between kangaroos and wombats for food (in terms of nutritional quality) is likely to minimise dietary overlap and hence the potential for competition between these sympatric taxa.

8.5 COPING WITH A FLUCTUATING ENVIRONMENT

8.5.1 Digestive and Feeding Strategies

Wombats live in environments that are seasonally or intermittently productive. Food resources at Riamukka SF declined in abundance and quality (via a change in species composition in pasture biomass rather than nutritional changes within species) during the cool dry winter (Chapter 4). Wombats were apparently unable to maintain a similar level of energy intake between good and poor seasons, as indicated by the seasonal changes in the level of FMR. It is probable that wombats use 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. As outlined in Chapter 1, if wombats were conventional herbivores, they might be expected to cope with seasonal changes in the quality and abundance of food resources by increasing their feeding selectivity for higher quality food items during poor seasons to maintain dietary quality. This did not appear to be the case in this study, as wombats did not increase feeding selectivity from amongst the sward during the poor season, nor did they shift their feeding areas between seasons (ie. switching to swards containing a higher proportion of good-quality items). However, wombats would benefit from seasonally switching areas for feeding only if the relative quality ranking of areas/swards within their home-ranges varied between seasons, and this may not have been the case at the Riamukka SF study site.

Instead of attempting to maintain dietary quality in the face of declining food quality, wombats decreased their overall feeding selectivity during the ‘poor’ season. Interestingly, though wombats during the good season showed increased selectivity for good-quality food species, increased selectivity was also shown for some relatively poor-quality species such as *Poa*. Also ingested during summer were significant amounts of seedhead (which comprised up to 32% of the diet during one summer) and, though selectivity for plant part was not assessed during this study, qualitative observations of

seedhead availability suggest that wombats were selecting for this dietary item. The dietary strategy used by wombats to cope with seasonal fluctuations in food quality is probably to maximise the efficiency of energy extraction from relatively high-quality food resources during the good season (as the hindgut digestive strategy is suited to efficient use of food items concentrated in cell contents). Rather than maintain dietary quality through increased feeding selectivity during the poor season, wombats appear to relax selectivity (possibly to help maintain dietary intake at the expense of good-quality food items) and delay digesta passage for more complete fermentation of fibre. Delayed digesta passage means wombats must accept a lower rate of energy absorption, but are able to do so because of low mass-specific energy requirements. Wombats clearly exhibit a high degree of flexibility in their use of food resources, yet their low energy requirements and digestive strategies enable them to exploit the stable and usually ‘poor quality’ pasture components as dietary staples.

8.5.2 Physiological Strategies

Wombats might be expected to use stored nutrient and energy reserves (fat, protein and glycogen) during periods of energy intake deficit, particularly since the hindgut strategy is suited to maximising the efficiency of energy extraction during good seasons and low FMR means that stored reserves should last longer during poor seasons. Wombats were apparently able to maintain a similar level of body condition (body mass and percentage of body fat) irrespective of season, suggesting that stored energy reserves are not a major source of energy during periods of energy deficit in normal (non-drought) years (Chapter 7). Wombats might also be expected to use the ‘good’ season as the period for most growth, and this may partially account for interseasonal differences in FMR.

8.5.3 Behavioural Strategies

The energetic cost of activity (i.e. movement) is an important, and to some extent facultative component of an animal’s overall energy expenditure, and for some animals may form the greatest component of FMR. The energetic costs of activity are likely to be more easily varied than those due to BMR, growth, reproduction, etc. In this study,

seasonally low activity (movement) levels in southern hairy-nosed wombats corresponded with seasonally low FMR, suggesting that southern hairy-nosed wombats were varying FMR largely by varying activity level. Wombats are able to minimise the costs of activity by spending long, inactive periods in a predator-proof burrow.

Wombats ‘switched off’ their activity during the poor season to reduce their energy expenditure. Southern hairy-nosed wombats reduced their intensity of activity during the poor season to about half that of the good season, and this was associated with a reduction in FMR of similar magnitude. The other two species showed a similar pattern in seasonal levels of FMR to southern hairy-nosed wombats. Despite probable lower activity levels during the poor season, common wombats did not appear to vary their ranging behaviour (size of home ranges and core areas), suggesting the importance of maintaining the size of feeding areas or other factors such as the number of burrows used.

Costs of activity are also minimised when outside the burrow through conservative ranging behaviour (e.g. use of habitual pads to minimise travel time, and small range area), and by not actively defending home-ranges and burrows (Chapter 5).

8.6 EVOLUTION OF THE VOMBATIDAE

As detailed in Chapter 3, at least ten species of wombats have been described from the Miocene, Pliocene and Pleistocene, with some species representing ‘giant’ (250 kg plus) forms. The earliest forms of wombats, including some giant forms such as *Phascolonus gigas*, were present during the late Oligocene (ca. 23 mya+) when Australia was largely covered in tropical forests; grasslands and shrublands did not spread across Australia until the Pliocene (1.9 to 5 mya). All early wombat forms for which there are post-cranial remains show evidence of scratch-digging ability (the humerus is similar to modern wombats and is characteristic of other scratch-digging mammals) (Murray 1998). Similar to modern wombats, all previous forms have high-crowned molars indicative of a fibrous diet. Contrary to the general perception that wombats evolved as grazers in grass-dominated habitats, early wombats appear to have evolved in the mostly grassless, tropical forests of Australia as scratch-digging (possibly fossorial) herbivores eating

fibrous plants of the understorey. Although giant wombat forms existed, most of the early forms were of comparable size to the modern wombats. *Warendja wakefieldi*, however, was a small, slender ‘rabbit-like’ wombat that co-existed with the extant species during the late Pleistocene. Murray (1998) suggests that *Warendja* was a selective feeder, occupying a niche in the Pleistocene similar to that of rabbits today. It is possible that extant Vombatids descended from ancestral larger forms, though phylogenetic evidence is scant. Murray (1998) believes that *Warendja* represents a survival from a primitive wombat lineage, and therefore might represent the ancestral wombat form. Modern wombats share characteristics with extant very large grazing herbivores, such as teeth suited to a fibrous diet and a large colon for fermentation of fibre. Johnson (1998) proposes that modern Vombatids are descended from larger grazing/browsing forms and that fossoriality was acquired as body size decreased. He argues that the key element for a large burrowing herbivore such as a wombat is the ability to deal with a low fibre diet, and that it is more plausible that wombats retained such ‘large-herbivore adaptations’ (ie. high crowned molars and colon fermentation) from a larger grazing mammal that was able to scratch-dig (pre-adapted to burrowing), rather than to have retained fossoriality after evolving from a smaller burrowing mammal and somehow acquiring ‘large-herbivore grazing adaptations’.

Why two genera of modern wombats survived the upheavals of the Pleistocene when other wombat forms and diprotodontoids became extinct can only be speculated upon. Perhaps a body-size comparable to that of modern wombats was critical in enabling fossoriality. The use of burrows and nocturnal emergence might have enabled wombats to escape hunters, or burrows provided a buffer against daily temperature extremes during cool climatic periods.

Of more relevance is what limits the distribution of extant wombats; they are not found in New Guinea, the grasslands of Northern or Western Australia, nor in Central Australia, yet macropodoids occur in all of these habitats. Possibly the distribution of wombats is limited by the stability or minimum density of grasses. Given that wombats are constrained in foraging by burrow locations and by conservative ranging behaviour, it makes sense that wombats may not be able to survive in areas of low pasture density (either seasonally or intermittently). However, this does not explain why wombats are

not in the grasslands of the tropical north or Western Australia. Cooke (1998) proposes that rabbits have modified native pastures to such an extent in some areas that sympatric common wombats cannot maintain populations. This suggests that competition from more mobile herbivores may be critically important to the ‘sedentary’ wombats. If this is the case, then landscape modifications (altered fire regimes) by Aboriginals to favour macropods in many grasslands throughout Australia might have been detrimental to wombats. Clearly, further research is required to address such hypotheses.

8.7 GENERALISED ALLOMETRIC REGRESSIONS

There is a paucity of data available on FMR for species of medium to large body mass. Consequently, regression analyses that seek to provide generalised allometric equations predicting FMR as a function of body mass suffer from possible bias in the regression coefficient. This problem is more pronounced when subsets of the data are being considered, such as those commonly based on taxonomy (eg. marsupial or eutherian) or habitat (eg. xeric or mesic). Similarly, season can profoundly influence FMR and water turnover rate in mammalian herbivores, yet few studies involving these parameters have been conducted on the same species in more than one season. The currently used allometric equations predicting FMR and WTR include data for some species that are seasonally biased, introducing possible bias into the overall regression equation. This study has highlighted the importance of taking into account seasonal influences in regression equations involving FMR. In an attempt to overcome such problems, Green (1997) reviewed the available data on field water fluxes in marsupials, and was able to separate seasonal and taxa effects and derive equations predicting water influx for macropodoid and non-macropodoid herbivores during dry or wet seasons. The validity of the regression approach to determining generalised allometric equations amongst taxa has been questioned because taxonomic groups differ in their level of interrelatedness, and thus data points used in such regressions differ in their level of independence to one another.

Despite possible shortcomings of allometric regression analyses for predicting ‘mean’ FMR values among taxa, these equations nevertheless have utility for examining concepts such as energy ‘maximisation’ vs ‘minimisation’ and possible underlying

ecological strategies. As outlined in Chapter 1, FMR is strongly influenced by body mass, and meaningful comparisons can only be made by using techniques that take into account body mass. Regression analyses enable this relationship to be quantified and, where data are scarce or unavailable, facilitate predictions to be made of FMR. Species with FMR that deviates markedly from the mean or expected value for a given body mass suggest adaptations that are unusual in terms of ecological energetics.

8.8 MANAGEMENT

The results of this study and others (Wells 1973; Johnson 1991a; Barboza 1993) suggest that management of wombat populations should seek to provide adequate food resources year-round within close proximity to burrows. Obligate burrow use constrains wombats to such areas for feeding, and greater distances travelled to food resources are likely to incur greater energy costs - an important consideration during dry periods or drought. Major threats to adequate food resources close to burrows are likely to be competition from more mobile species with overlapping diets, such as macropodids and domestic stock (particularly in arid regions where stock have access to water and urea), and land changes due to intensive agriculture. It is not known whether wombats recolonise areas where populations have perished and burrows are in an unusable state (collapsed). If wombats depend on established burrows, habitual pads and grazed "lawns", then dispersal (and hence establishment of new populations) may be possible only in special circumstances. Therefore, the loss of sub-populations should be seen as being possibly irreversible (at least without extensive human intervention). Interference (trapping, handling etc.) affects the behaviour of wombats, and most likely causes stress. Research and management programs should be aware of the possible effects of such interference on the behaviour and wellbeing of animals, and as causing bias of research results.

8.9 A UNIQUE ADAPTIVE SYNDROME?

Undoubtedly, an energetically frugal lifestyle enables wombats to exist in their characteristically harsh and poor-quality habitats. In Chapter 1, I presented an

hypothesised adaptive syndrome for energy conservation in wombats. The results of this study suggest that this syndrome exists in wombats. Many species of mammalian herbivore use adaptations that have advantages in terms of energy conservation (such as burrowing) or that enable them to exploit poor quality food resources (such as large body size or hindgut fermentation), but it is the combination of these adaptations (and others) that make the syndrome unique in wombats. Wombats represent the extreme body-size for a burrowing mammalian herbivore. The use of burrows and an inherently low BMR apparently enable wombats to achieve their seasonally exceptionally low FMR for their body size. Low energy requirements, powerful mastication and hindgut fermentation enable wombats to use poor-quality (but abundant and stable) fibrous grasses as a dietary staple. Low energy requirements and use of burrows enables wombats to achieve low WTR, and consequently the ability to exploit grasses that are dry (as well as poor quality) in the absence of drinking water. In contrast to the proposed hypothesis, wombats do not appear to make extensive use of stored reserves to compensate for energy intake deficit during the poor season. Instead, wombats balance their energy expenditure with their energy intake, and this is mostly achieved by ‘switching off’ activity. The unique adaptive syndrome of these extraordinary animals enables them to ‘bend the rules’ of the general relationship between body mass and energy expenditure.