Marsupial Nutrition

Marsupial Nutrition describes the food resources used by marsupials as diverse as small insectivores and large folivores. It discusses the ways in which their digestive systems and metabolism are designed to cope with foods as different as nectar and fungus, tree sap and tough perennial grasses, and insects and eucalypt foliage. Although the subject species are marsupials the general principles of nutritional ecology and digestive strategies that are introduced at the beginning of the chapters are applicable to all mammals. Advanced undergraduates and graduate students at all levels in the areas of vertebrate zoology, nutrition, ecology and digestive physiology will find *Marsupial Nutrition* particularly instructive. Wildlife biologists, veterinarians and nutritionists will also find much of interest.

IAN D. HUME is Challis Professor of Biology at the University of Sydney. He has carried out research in the field of comparative nutrition in the USA, Germany, Sudan and Japan, as well as in Australia. His book *Digestive Physiology and Nutrition of Marsupials* (1982) won the Whitley Award for Best Text Book from the Royal Zoological Society of New South Wales. He has also co-authored *Comparative Physiology of the Vertebrate Digestive System* (1995), and co-edited *Possums and Gliders* (1984), and *Kangaroos, Wallabies and Rat-kangaroos* (1989). Professor Hume is currently a managing editor of *Journal of Comparative Physiology B* and his research has been widely published in many international journals.

Marsupial Nutrition

Ian D. Hume

Challis Professor of Biology
University of Sydney
Australia

Contents

Contents

Preface

Marsupial Nutrition is about the nutritional ecology and digestive physiology of marsupials. The nutritional ecology of a species describes the interface between animals of that species and their food resources. Their digestive physiology determines which resources in the environment are food. The roots of *Marsupial Nutrition* lie in its predecessor, *Digestive Physiology and Nutrition of Marsupials*, published in 1982, but the great increase in knowledge and understanding of the nutritional niches filled by marsupials, and their digestive strategies, over the last 16 years has led to a much more comprehensive treatment of marsupial groups, their nutritional ecology and their digestive physiology in the present book.

Nevertheless, the reasons for writing *Marsupial Nutrition* remain the same: to inform physiologists and nutritionists about how the digestive systems of marsupials work, and to help zoologists and wildlife managers understand how food resources in the environment are utilised by various groups of marsupials, and which elements of the landscape are likely to be critical to the well-being of populations of marsupials in terms of their nutrition.

The ecological niches filled by marsupials are many and varied. Marsupials include many more species and forms than just kangaroos and koalas. In fact there are approximately 180 species of marsupials in Australia and New Guinea, 78 in South America and 1 in North America. They range in body size from 3 g shrew-like planigales (*Planigale* spp.) to 70 kg red kangaroos (*Macropus rufus*). They are found in habitats as diverse as freshwater streams (*Chironectes minimus*, the water opossum of South America), alpine areas (*Burramys parvus*, the mountain pygmy-possum of south-eastern Australia), hot deserts (*Notoryctes*, the marsupial moles of central Australia) and tropical rainforests (dorcopsis wallabies of New Guinea). Their diets range from purely insects to vertebrates, fungi, underground plant roots, bulbs, rhizomes and tubers, plant exudates such as saps and gums, seeds, pollen, terrestrial grasses, herbs and shrubs and tree foliage. Adaptive features of marsupials often have analogues in eutherian (placental) mammals. These are examples of convergent evolution. Some of the convergences are obvious: the marsupial gliders resemble the flying squirrels and lemurs, the Tasmanian tiger or thylacine was dog-like, and marsupial moles are reminiscent of eutherian moles. Other convergences are at the physiological level. For instance, ringtail possums produce two types of faeces and consume only the soft faeces that are higher in nutrient content; eutherian rabbits do the same. The wombats process grasses and sedges in a greatly

enlarged colon, as do horses. Numbats feed on termites in much the same way that some eutherian anteaters do.

Marsupial Nutrition opens with a general chapter on metabolic rates of marsupials and their requirements for energy and nutrients such as water and protein. I deal principally with nutrition of the adult animal, and generally include the young only in so far as it affects the energy and nutrient requirements of adults (usually the lactating female). The next seven chapters deal with various groups of marsupials on the basis of their dietary and thus gastrointestinal tract specialisations. They begin with the relatively simple, the carnivores/insectivores, then progress through omnivorous groups to the most complex (several groups of herbivores). Most chapters open by introducing one or more general nutritional concepts pertinent to that part of the book. These concepts hopefully provide the framework for the rest of the chapter that follows. Most chapters conclude with a section on the nutritional ecology of each dietary group. The kangaroos and wallabies are an exception, for a separate chapter is devoted to their dietary niches and nutritional ecology. Chapter 9 provides an opportunity to review and compare the foraging and digestive strategies of the various groups of marsupials in the context of current thinking about marsupial evolution and the possible evolution of digestive strategies in mammals. The final chapter contains suggestions about where research in marsupial nutrition should head in the twenty-first century.

Readers familiar with its predecessor will notice that the material covered in *Marsupial Nutrition* is much more balanced in its treatment of carnivorous, omnivorous and herbivorous marsupials. This is because of the expanded research effort that has gone into marsupials other than kangaroos over the last 16 years. It has also been pleasing to be able to describe the work of, and refer to, many more South American authors than previously. Hopefully this book will stimulate further comparative studies on the digestive physiology, nutritional ecology and metabolism of a still wider range of species from South America in the future.

Within Australia, greater research effort recently has gone into marsupials from more mesic environments. Former research had been concerned more with arid-zone marsupials, not surprisingly so as two-thirds of the Australian land surface is classified as semi-arid or arid. Hopefully the greater coverage of more mesic forms in *Marsupial Nutrition* will stimulate even more studies on a wider range of species from across the broad spectrum of environments from rainforest to desert. Research on the nutrition and metabolism of New Guinean marsupials still lags, but again, recent work brought together in *Marsupial Nutrition* may also stimulate greater research effort on these fascinating animals.

The classification of marsupials to family level adopted in this book is based on that of Woodburne & Case (1996), and to species level on Eisenberg (1989), Redford & Eisenberg (1992), Strahan (1995) and Flan-

nery (1995). In three cases of Australian species I have deviated from Strahan (1995) on the basis of new information. Two species of marsupial moles are now recognised: *Notoryctes typhlops* (southern marsupial mole) and *N. caurinus* (northern marsupial mole) (Maxwell, Burbidge & Morris 1996). The kowari (formerly *Dasyuroides byrnei*) is now subsumed in the genus *Dasycercus* as *D. byrnei* (Maxwell *et al.* 1996). *Antechinus agilis* (agile antechinus) is recognised as a species separate from *A. stuartii* in southern Victoria and south-eastern New South Wales (Dickman *et al.* 1988). The common names used for American species are based on Eisenberg (1989) and Redford & Eisenberg (1992). The common names used for Australian species are based on Strahan (1995), and those for New Guinean species on Flannery (1995). A list of the marsupial species mentioned in the text, with scientific and common names, will be found in the Appendix.

Because of the very recent nature of some of the information contained in this book I have depended heavily on the work of several current graduate students and on that of other colleagues who have generously supplied me with unpublished manuscripts or manuscripts in the process of publication. For allowing me access to their unpublished results, I thank Chris Allen, Bruce Bowden, Don and Felicity Bradshaw, Terry Dawson, Chris Dickman, Bart Eschler, Tim Flannery, Bill Foley, Lesley Gibson, Ross Goldingay, Perdita Hope, Menna Jones, Chris Johnson, Jonathan Kingdon, Steve Lapidge, Ivan Lawler, Geoff Lundie-Jenkins, Diego Moraes, Kylie McClelland, Diane Moyle, David Pass, Georgina Pass, Ken Richardson, Myfanwy Runcie, Felix Schlager, Andrew Smith, Ian van Tets and Mike Wolin.

I am also appreciative of colleagues who have commented on sections of the book: Perry Barboza, John Calaby, Terry Dawson, Chris Dickman, Tim Flannery, Graham Faichney, Bill Foley, Ed Stevens, and Pat Woolley.

Frank Knight provided the silhouettes of each species appearing in the figures, and most of the figures. Paulette Ripikoi and Sylvia Warren assembled most of the tables and references. My wife Desley provided the moral support needed to bring the book to fruition. To all these people my heartfelt thanks.

Ian Hume
Sydney

1 Metabolic rates and nutrient requirements

1.1 CONCEPTS

This chapter deals with energy and nutrient requirements of marsupials, and how these are related to and can often be predicted from basal metabolic rates. The rest of the book deals with the dietary and foraging habits of the various groups of marsupials, and how food is processed by the animal. Food processing involves prehension and cutting, tearing, crushing or grinding by the teeth, digestion and absorption by the gut, and metabolism of absorbed nutrients in the liver and other body tissues. Available information on all of these aspects of the nutrition and nutritional ecology of marsupials is discussed. The chapters are organised so that the relatively simple digestive systems of carnivorous marsupials are covered first, followed by the more complex systems of omnivores and finally the most complex digestive systems which are found in the herbivores. Problems of defining carnivory, omnivory and herbivory are dealt with in Chapter 2; suffice to say here that for an appropriate sequence of chapters this 'division' of feeding types is convenient and widely understood among biologists.

1.1.1 Nutritional niche

Central to this book is the concept of the nutritional niche of an animal. Hutchinson (1957) introduced the concept of niche width of an organism. Kinnear *et al.* (1979) applied the concept to herbivores, and demonstrated how symbiotic gut microorganisms effectively expanded the host animal's niche width.

Fig 1.1, adapted from Kinnear *et al.* (1979), shows the fundamental and realised nutritional niches of a herbivore. The *fundamental nutritional niche* of an animal is described by the range of nutrient concentrations between the minimum required and the maximum tolerated by the species. It is defined in this example by two dimensions, each linearly ordered on the X and Y axes. The lower limits of the dimensions denote the minimum concentrations of each nutrient (for example, an essential amino acid on X and an essential fatty acid on Y) required by the animal. The upper limits denote the maximum levels that can be tolerated without toxicity symptoms appearing. The area, or 2-space (Kinnear *et al.* 1979), so defined, describes the limits within which the species can survive and persist. A third axis, representing another nutrient, could be added to define a volume or
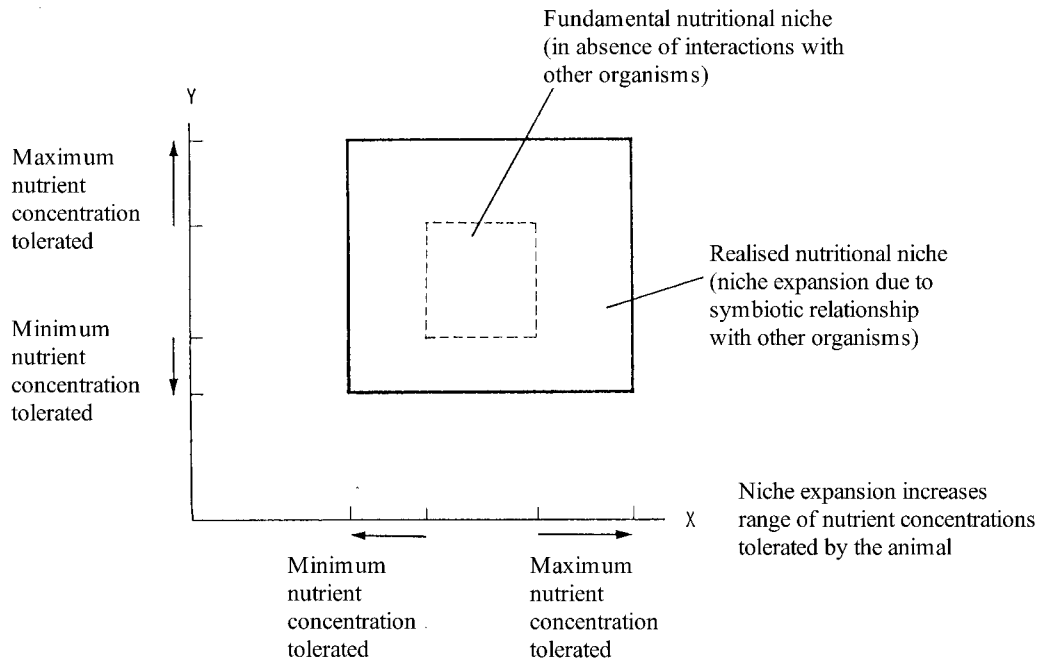
Figure 1.1 The fundamental and realised nutritional niche of an animal, showing the concept of niche expansion due to symbiotic relationship with other organisms. Adapted from Kinnear *et al.* (1979).

3-space, and n axes would define a hypervolume (Hutchinson 1957), and thus a species' fundamental nutritional niche.

The *realised nutritional niche* of an organism is a modified range of nutrient concentrations that can be used by the species because of interactions with other organisms. In the case of the herbivore this means the symbiotic microorganisms resident in its gut. These interactions include biosynthesis of essential nutrients and catabolism of many potentially toxic compounds, and render the host animal more tolerant of both deficiencies and excesses of several nutrients. This is an example of nutritional niche expansion. It expands the range of resources within the environment that the host animal can use as food.

The converse, nutritional niche contraction, results from competition. For instance, a herbivore may be effectively prevented from using highly nutritious food by more efficient competitors, in this case non-herbivores. By harbouring symbiotic microbiota in their gut, herbivores have introduced an additional link into the food chain, which inevitably leads to material and energy losses. Animals without this additional link have an advantage if the food can be digested by the animal's own enzymes (catalytic digestion), but herbivores have an advantage if the food can be digested only autocatalytically (that is, by microbial fermentation). So we find that herbivores usually are associated with poorer quality food resources than non-

herbivores even though they are capable of using both good and poor quality foods.

To place the concept of nutritional niche within the framework of this book, a useful working statement is that an animal's nutritional niche can be defined principally by: (a) what it needs in the way of energy and specific nutrients; and (b) how it harvests and extracts those needed nutrients from the food resources available in its nutritional environment. In general, specialist feeders such as carnivores and folivores have narrower nutritional niches than have omnivores and generalist herbivores.

1.2 METABOLIC RATES

Energy and thus food requirements are related to metabolic rate. Three measures of rate of metabolism are relevant here: basal metabolic rate (BMR), field metabolic rate (FMR) and maximum sustained metabolic rate.

The basal metabolic rate of an endotherm is the minimum rate of metabolism compatible with endothermy (McNab 1988b). It can be measured as the rate of oxygen consumption (or heat production) of a non-reproductive, post-absorptive adult animal at rest (but not asleep) in its thermoneutral zone and not experiencing any physical or psychological stress. Some of these conditions are easier to satisfy than others; in herbivores a truly post-absorptive state is never reached without starving the animal because of the continuous nature of digestive function in these animals. Standard metabolic rate (SMR) is the equivalent minimal metabolic rate in an ectotherm at a particular temperature (Withers 1992a).

Field metabolic rate is the energy cost of free existence. It includes basal metabolism along with the costs of maintenance, thermoregulation and activity (Nagy 1994). However, measurements of FMR often include other costs associated with tissue growth, fat storage and reproduction. The latter may include additional activity costs involved with defence of breeding territories, courtship and foraging on behalf of the young. For these reasons FMRs are much more variable for a species than are BMRs. Thus, although FMRs relate directly to the real world, BMRs are widely used for comparisons across species and higher taxons.

The maximum sustained metabolic rate is the highest rate of energy expenditure that an animal can sustain from food intake, without using body energy stores. It has been measured experimentally in small mammals by using combinations of physical activity, cold stress and lactation (Hammond *et al.* 1994).

1.3 BASAL METABOLIC RATES

Body mass is the major determinant of energy use in endotherms (Nagy 1987, 1994). In eutherian mammals basal energy metabolism has been

shown to vary with body mass according to the equation BMR = a Mass^b . The most appropriate value for the power function 'b' is the subject of much continuing debate. Withers (1992a) summarised the allometric relationships between metabolic rate and body mass for various groups of animals from unicells to vertebrates, and the various arguments for predicting what the power function should be, including that based on geometric similarity. In this theory, as most metabolic activities occur at surfaces, metabolic rate should increase as the square power, whereas body mass increases as the cube power of body size. Thus to compare the BMR of animals of different body size the discrepancy between surface area increase and volume increase should be accommodated by raising body mass to the two-thirds power (i.e. Mass $^{0.67}$), assuming the animal to be a perfect sphere. However, this is rarely the case, and empirically the power function that best fits available data from the smallest to the largest animals has been found to be generally between 0.5 and 1.0, averaging close to 0.75 for interspecific relationships and 0.72 for intraspecific relationships (Withers 1992a).

A more recent model of scaling in energy metabolism is based on the idea that living systems are sustained by the transport of essential materials through space-filling fractal networks of branching tubes. In this model, the terminal tubes do not vary with body size and the energy required to distribute resources through this network is minimised (West, Brown & Enquist 1997). This model suggests that most metabolic functions of animals should be related to body mass by some multiple of the one-quarter power, and that for whole-body parameters the power function should be close to three-quarters because most animals are three-dimensional.

Early work using whole-animal calorimetry yielded interspecific relationships to the power of 0.73 when Brody (1945) used 14 eutherian and 6 avian species, or 0.75 when Kleiber (1961) used 12 eutherians. In each case the work can be criticised for insufficient numbers of animals, inadequate representation of mammalian and avian taxons, and incorrect statistical analysis. A more recent analysis of a much broader data set (248 eutherian species and 42 marsupials) by Hayssen and Lacy (1985) yielded interspecific power functions of 0.70 for eutherians and 0.75 for marsupials. Importantly, interspecific relationships within orders or families often deviated significantly from these power functions. For example, 'b' for 16 heteromyid rodents was 0.91, but for 27 sciurids it was 0.61.

These criticisms notwithstanding, the power function of 0.75 is widely used for interspecific comparisons of metabolic rates and other physiological variables among subsets of eutherian taxons, and for statistical analysis data are often tested for significant deviation from the 'Kleiber line'. When body mass is expressed in kg, the Kleiber line yields a value for 'a' (the intercept) of 70 if the BMR is expressed in kcal kg$^{-0.75}$ d^{-1}, 293 if the BMR is in kJ kg$^{-0.75}$ d^{-1}, or 3.34 if the BMR is in the SI (Système International d'Unités) units of Watts kg$^{-0.75}$.

4

The traditional view, from Dawson and Hulbert's (1970) comparison of eight Australian marsupial species from five families, has been that the BMR of marsupials is about 30% below that of eutherian mammals. We now know that this is an oversimplification, yet, despite the small number of species represented, Dawson and Hulbert's (1970) 'marsupial line' is still often used as a standard against which other marsupials are compared as the data become available. Their line yields a BMR for the 'average marsupial' of 49 kcal or 204 kJ $kg^{-0.75}$ d^{-1} or 2.33 W $kg^{-0.75}$.

The concept of an average marsupial BMR and a strong taxonomic difference in BMRs between marsupials and eutherians has been challenged by McNab (1978; 1986; 1988b), who concluded that variations in BMR among both marsupials and eutherians are strongly correlated with food habits, activity level and the precision of temperature regulation. In both groups of mammals, feeding on fruit, tree foliage or invertebrates is associated with low BMRs, especially at large body size. This is because these food resources are seasonally unavailable (fruit, invertebrates), poorly digested (tree leaves) or have to be detoxified (tree leaves, some invertebrates). In addition, frugivory and folivory are associated with sedentary, arboreal habits in both mammalian groups. Correlations have also been demonstrated between low mammalian BMRs and fossoriality (burrowing), nocturnal habits and reduced muscle mass (as seen in many arboreal species (McNab 1992)). The question of whether phylogeny or food habits and activity is more important in determining BMR is unresolved, and is likely to remain so until many more marsupial and eutherian species from a wider range of nutritional habitats are examined. At present, the balance of opinion seems to be that there is a basic underlying difference in BMR between eutherians and marsupials (and monotremes), but that the influence of other factors such as food habits and activity is sometimes strong enough to mask phylogeny.

Table 1.1 summarises available data on BMRs of marsupials. Marsupial BMRs tend to form a tight cluster, with about half of the values falling between 65 and 74% of the value expected from an equivalent body mass in eutherians. There are only a few high values, the highest being those of very small species such as the 7 g *Planigale ingrami* (106%) and the 10 g honey possum (*Tarsipes rostratus*) (158%). McNab (1978) also reported a high BMR for the didelphid *Chironectes minimus* (98% of the Kleiber mean), which he attributed to the high rates of heat loss in a semi-aquatic environment. Similarly, among the monotremes, the BMR of the semi-aquatic platypus (*Ornithorhyncus anatinus*) (67% of the Kleiber mean) is higher than that of the terrestrial echidnas *Tachyglossus* (31%) and *Zaglossus* (27%) (Dawson, Grant & Fanning 1979). However, Thompson (1988) re-evaluated the BMR of *Chironectes* and found it to be 64%, not 98%, of the Kleiber mean, and concluded that *Chironectes* was not an exception to the pattern of low BMRs within the Marsupialia. Similarly, Elgar & Harvey (1987) felt

Table 1.1. *Basal metabolic rates (BMR) of marsupials*

Species	Body mass (g)	mLO$_2$ g^{-1} h^{-1} [a]	kJ kg$^{-0.75}$ d^{-1} [b]	W kg$^{-0.75}$[c]	%[d]	Ref.
		BMR				
Family Didelphidae						
Marmosa microtarsus	13	1.436	244	2.78	83	1
Monodelphis brevicaudata	76	0.800	211	2.41	72	2
Monodelphis domestica	104	0.608	161	1.83	55	3
Marmosa robinsoni	122	0.800	238	2.71	81	2
Caluromys derbianus	331	0.685	262	2.99	89	2
Metachirus nudicaudatus	336	0.610	234	2.67	80	2
Philander opossum	751	0.450	211	2.41	72	2
Lutreolina crassicaudata	812	0.500	239	2.72	82	2
Chironectes minimus	946	0.580	288	3.28	98	2
Didelphis marsupialis	1329	0.460	249	2.84	85	2
Didelphis virginiana	2403	0.380	238	2.71	81	2
Family Dasyuridae						
Planigale ingrami	7	2.130	310	3.53	106	4
Planigale gilesi	10	1.357	214	2.44	73	4, 5
Planigale maculata	11	1.135	184	2.10	63	6, 7
Sminthopsis crassicaudata	14	1.330	231	2.63	79	6, 8, 9
Antechinomys laniger	24	0.980	195	2.22	67	6
Antechinus stuartii	28	1.278	263	3.00	90	6, 8, 10
Pseudantechinus macdonnellensis	43	0.630	145	1.65	49	6
Dasycercus cristicauda	93	0.505	140	1.60	48	6, 9
Dasycercus byrnei	102	0.760	216	2.46	74	5, 6
Phascogale tapoatafa	157	0.810	257	2.93	88	6
Dasyurus hallucatus	584	0.510	225	2.57	77	6
Dasyurus viverrinus	910	0.450	222	2.53	76	6
Dasyurus geoffroii	1100	0.405	209	2.38	71	11
Dasyurus maculatus	1782	0.330	192	2.19	66	6
Sarcophilus harrisii	5050	0.280	212	2.42	72	6
Family Myrmecobiidae						
Myrmecobius fasciatus	400	0.356	143	1.63	49	12
Family Peramelidae						
Isoodon auratus	428	0.346	138	1.57	47	13
Perameles nasuta	667	0.479	209	2.38	71	8, 14
Isoodon macrourus	1185	0.414	201	2.29	69	8, 14
Macrotis lagotis	1266	0.353	169	1.93	58	14, 15

6

Table 1.1. *cont.*

Species	Body mass (g)	BMR				Ref.
		mLO$_2$ g^{-1} h^{-1} [a]	kJ kg$^{-0.75}$ d^{-1} [b]	W kg$^{-0.75}$ [c]	%[d]	
Family Peroryctidae						
Echymipera kalubu	695	0.495	218	2.49	74	14
Echymipera rufescens	836	0.470	210	2.39	72	14
Family Phascolarctidae						
Phascolarctos cinereus	4700	0.217	161	1.84	55	16
Family Vombatidae						
Lasiorhinus latifrons	29 920	0.110	130	1.48	44	17
Family Burramyidae						
Cercatetus nanus	70	0.860	223	2.54	76	18
Family Petauridae						
Petaurus breviceps	128	0.692	209	2.38	71	8
Gymnobelideus leadbeateri	166	0.620	199	2.27	68	19
Family Pseudocheiridae						
Pseudocheirus peregrinus	890	0.534	266	2.80	91	20
Pseudocheirus occidentalis	917	0.474	234	2.67	80	15
Petauroides volans	1000	0.417	210	2.39	72	21
Family Tarsipedidae						
Tarsipes rostratus	10	2.900	463	5.28	158	22
Family Acrobatidae						
Acrobates pygmaeus	14	1.067	185	2.11	63	23
Family Phalangeridae						
Trichosurus vulpecula	1982	0.315	188	2.14	64	8
Spilocuscus maculatus	4250	0.240	174	1.98	59	24
Family Potoroidae						
Potorous tridactylus	1035	0.455	231	2.63	79	25
Bettongia penicillata	1070	0.460	236	2.69	81	25
Aepyprymnus rufescens	2870	0.401	263	3.00	90	25
Family Macropodidae						
Lagorchestes conspicillatus	2260	0.320	206	2.35	70	26
Setonix brachyurus	2940	0.304	201	2.29	69	15
Macropus parma	3750	0.367	257	2.93	88	27
Thylogale thetis	4400	0.318	232	2.64	79	27

Table 1.1. (*cont.*)

Species	Body mass (g)	BMR				Ref.
		mLO_2 g^{-1} h^{-1} [a]	kJ $kg^{-0.75}$ d^{-1} [b]	W $kg^{-0.75c}$	%[d]	
Family Macropodidae (*cont.*)						
Macropus eugenii	4878	0.283	212	2.42	72	7, 27
Dendrolagus matschiei	6960	0.205	168	1.92	57	28
Macropus robustus erubescens	30 000	0.178	210	2.40	72	29
Macropus rufus	28 745	0.184	209	2.38	71	7, 29

Note: [a] Mass-specific rate or metabolic intensity

[b] Energetic equivalence of $O_2 = 21$ kJ L^{-1} (Withers 1992b)

[c] W = 87.72 kJ d^{-1}

[d] Percentage of predicted value from Kleiber's (1961) equation for eutherians. The 'marsupial mean' is 70% of the eutherian (Dawson & Hulbert 1970).

Source: 1. Morrison & McNab 1962; 2. McNab 1978; 3. Dawson & Olson 1988; 4. Dawson & Wolfers 1978; 5. Dawson & Dawson 1982; 6. MacMillen & Nelson 1969; 7. Morton & Lee 1978; 8. Dawson & Hulbert 1970; 9. Kennedy & Macfarlane 1971; 10. Wallis 1976; 11. Arnold & Shield 1970; 12. McNab 1984; 13. Withers 1992b; 14. Hulbert & Dawson 1974a; 15. Kinnear & Shield 1975; 16. Degabriele & Dawson 1979; 17. Wells 1978a; 18. Bartholomew & Hudson 1962; 19. Smith *et al.* 1982; 20. Munks 1990; 21. Foley 1987; 22. Withers, Richardson & Wooller 1990; 23. Fleming 1985; 24. Dawson & Degabride 1973; 25. Wallis & Farrell 1992; 26. Dawson & Bennett 1978; 27. White, Hume & Nolan 1988; 28. McNab 1988a; 29. Dawson 1973.

that many associations between BMR and dietary category among mammals could equally be described by taxonomic affinities.

Among the lowest marsupial BMRs reported are those of several desert-dwelling species such as the dasyurids *Pseudantechinus macdonnellensis* (only 49% of the rate expected from mass in eutherians) and mulgara (*Dasycercus cristicauda*) (48%), the bilby (*Macrotis lagotis*) (Fig. 1.2) (58%), hairy-nosed wombat (*Lasiorhinus latifrons*) (42%) and golden bandicoot (*Isoodon auratus*) (47%). Also low are several arboreal folivores such as the koala (*Phascolarctos cinereus*) (52%), common spotted cuscus (*Spilocuscus maculatus*) (Fig. 1.3) (59%) and the tree kangaroo *Dendrolagus matschiei* (57%).

1.4 CONSEQUENCES OF A LOW METABOLIC RATE

One consequence of a low BMR is generally a low body temperature (Withers 1992a). A low metabolic rate also has several important consequences for animals in terms of nutrient requirements and thus the width of

Figure 1.2 The bilby (*Macrotis lagotis*), an arid-zone omnivorous marsupial with a basal metabolic rate substantially below that of most other marsupials. (Pavel German)

Figure 1.3 The common spotted cuscus (*Spilocuscus maculatus*), one of several arboreal folivorous marsupials with unusually low basal metabolic rates. (Pavel German)

their nutritional niche. Other consequences, in environmental tolerance and reproductive rate, are related not only to an animal's BMR but also to its metabolic scope, which is the extent to which it can increase metabolic rate above basal to accommodate high rates of heat loss in cold environments and the energetic costs of a high reproductive potential (McNab 1986; Dawson & Olson 1988). Nevertheless, we can confidently predict that a low BMR will mean lower food requirements for maintenance, and that energy reserves will last longer under adverse conditions.

1.5 MAINTENANCE ENERGY REQUIREMENTS OF CAPTIVE MARSUPIALS

In captive wild animals and housed domestic stock, energy additional to basal requirements is needed for feeding, drinking, digestion, absorption and metabolism of absorbed nutrients, and for postural changes, but little is needed for thermoregulation or other activities. Under these conditions, maintenance energy requirements are often approximately double the BMR for the species. Estimated maintenance energy requirements of captive marsupials are listed in Table 1.2. These estimates are from two sources. The first is from feeding experiments in which it is assumed that non-reproductive adult animals at or close to body mass balance eat enough energy to maintain their energy status but no more when offered food *ad libitum*. Total collection of faeces allows calculation of the intake of digestible energy. The second source is from indirect calorimetry measurements of rates of oxygen consumption, and assuming that these are equivalent to metabolisable energy. Metabolisable energy is then converted to digestible energy using appropriate factors. With few exceptions, maintenance requirements are in the range of 150–250% of BMR. There also appears to be a trend for maintenance requirement as a multiple of BMR to decrease with increasing body mass of the species. This may reflect both a greater activity increment and greater requirements for thermoregulation in the smaller species, even under captive conditions.

Comparisons with equivalent eutherians are hampered by a relative lack of data on maintenance energy requirements of captive eutherians. The study by Hume (1974) included sheep with euros and red kangaroos. The estimated maintenance requirement for digestible energy by the sheep was $569 \, \text{kJ} \, \text{kg}^{-0.75} \, \text{d}^{-1}$, which is 137% and 125% respectively of those of the euro and red kangaroo. Thus the approximately 30% difference in BMRs between macropodids and their eutherian counterparts, the ruminants, is maintained in maintenance energy requirements. Similarly, the maintenance energy requirements of eutherian carnivores such as the mink (*Mustela vison*) (Farrell & Wood 1968) and the red fox (*Vulpes vulpes*) (Vogtsberger & Barrett 1973) in captivity are significantly higher than those of the

Table 1.2. *Maintenance energy requirements of captive marsupials. Values given as digestible energy (DE)*

Species	Body mass (kg)	Maintenance requirement		Ref.
		kJ kg$^{-0.75}$ d^{-1}	% of BMR	
(a) Estimates from feeding (balance) experiments				
Rufous hare-wallaby (*Lagorchestes hirsutus*)	1.2	326	—	1
Eastern quoll (*Dasyurus viverrinus*)	1.3	545	246	2
Tasmanian devil (*Sarcophilus harrisii*)	3.8	545	257	2
Parma wallaby (*Macropus parma*)	3.8	504	196	3
Tammar wallaby (*Macropus eugenii*)	4.8	320	151	4
Red-necked pademelon (*Thylogale thetis*)	5.0	530	228	4
Koala (*Phascolarctos cinereus*)	5.8	388	241	5
	6.6	330	205	6
Eastern grey kangaroo (*Macropus giganteus*)	20.8	570	—	4
Hairy-nosed wombat (*Lasiorhinus latifrons*)	23.1	140	108	7
Euro (*Macropus robustus erubescens*)	27.0	414	130	8
Common wombat (*Vombatus ursinus*)	27.9	140	—	7
Red kangaroo (*Macropus rufus*)	30.0	456	192	8
(b) Estimates from calorimetry measurements[a]				
Greater glider (*Petauroides volans*)	1.0	580	276	9
Long-nosed potoroo (*Potorous tridactylus*)	1.0	529	229	10
Brush-tailed bettong (*Bettongia penicillata*)	1.1	540	229	10
Common brushtail possum (*Trichosurus vulpecula*)	2.3	370	197	11
Rufous rat-kangaroo (*Aepyprymnus rufescens*)	3.1	386	147	10
Parma wallaby (*Macropus parma*)	4.2	368	143	12
Tammar wallaby (*Macropus eugenii*)	4.5	309	146	12
Red-necked pademelon (*Thylogale thetis*)	4.9	389	168	12

Note: [a]Assumed to be equivalent to metabolisable energy (ME)
Corrected to digestible energy (DE) by the value for ME/DE of 0.95 derived by Wallis & Farrell (1992) for potoroine marsupials, except for the greater glider, which was corrected to DE by 0.55 by Foley (1987).
Source: 1. Bridie, Hume & Hill 1994; 2. Green & Eberhard 1979; 3. Hume 1986; 4. Dellow & Hume 1982a; 5. Ullrey, Robinson & Whetter 1981b; 6. Cork, Hume & Dawson 1983; 7. Barboza, Hume & Nolan 1993; 8. Hume 1974; 9. Foley 1987; 10. Wallis & Farrell 1992; 11. Harris, Dellow & Broadhurst 1985; 12. White, Hume & Nolan 1988.

two marsupial carnivores studied by Green & Eberhard (1979).

Higher energy expenditures have been reported by Cowan, O'Riordan & Cowan (1974) in the alpine dasyurid *Antechinus swainsonii* maintained in cages for eight weeks. At body mass maintenance their digestible energy intake was close to four times their calculated BMR. The authors interpreted this high maintenance estimate as representing the energy cost of

maintenance plus activity, as the animals were extremely active in their cages, and they concluded that this total energy expenditure was probably close to the normal energy demand of this species under free-living conditions.

1.6 VOLUNTARY FOOD INTAKE

The lower maintenance energy requirements of captive macropodid marsupials compared with housed domestic eutherian grazer/browsers are often reflected in lower voluntary food intakes of adult animals at or near body mass maintenance. This is illustrated in Table 1.3, which includes data from eight studies in which captive macropodids and ruminants were fed common diets of either chopped lucerne (alfalfa) hay or a chopped barley straw diet. Digestibility of dry matter is often higher in ruminants than in kangaroos (for reasons given in Chapter 6), which means that the difference between the two groups would be even greater if values were expressed as intake of digestible dry matter (equivalent to digestible energy).

1.7 FIELD METABOLIC RATES OF MARSUPIALS

Field metabolic rate, or the energy cost of free existence, is routinely measured by the use of doubly labelled water (Nagy 1980). Water labelled with the stable isotope of oxygen (^{18}O) and either the stable isotope of hydrogen (deuterium) or its radioactive isotope (tritium) is injected into the body water pool. After equilibration with the total body water pool, the rate of washout of the hydrogen isotope is a measure of water flux. The oxygen isotope traces both the water and carbon dioxide in the body, so the difference between washout rates of oxygen and hydrogen is a measure of CO_2 production (metabolic rate). Potential sources of error in the technique are discussed by Nagy (1980).

FMR has now been measured in 28 species of marsupials (Table 1.4). As mentioned earlier, FMR is much more variable within a species than is BMR. The main sources of variation can be readily identified from this table as being sex, season and reproductive state. Nagy (1987) analysed FMRs of 23 species of eutherians and 13 species of marsupials allometrically, and found that the slope of the regression equation relating FMR to body mass was 0.81 for eutherians but only 0.58 for marsupials. The latter exponent is used in Table 1.4. When plotted together the two regression lines cross each other. This means that, unlike BMR, a common scaling factor cannot be used to compare FMRs between the two therian groups. Nagy (1987) concluded that in the body size range of 240–550 g, FMRs of marsupials and eutherians are similar, while at lower body sizes FMRs of eutherians are lower. The only dietary comparison Nagy (1987) was able to make was within the herbivores, for which marsupials and eutherians both

12

Table 1.3. *Voluntary food intakes of macropodid marsupials and sheep fed chopped lucerne (alfalfa) hay and goats, euros and wallaroos fed a chopped barley straw diet. All values given as g dry matter kg $^{-0.75}$ d^{-1}*

Ruminant		Macropod		Ref.
71.7	(Sheep)	58.1	Red kangaroo (*Macropus rufus*)	Foot & Romberg (1965)
64.1	(Sheep)	38.7	Red kangaroo	McIntosh (1966)
66.5	(Sheep)	48.1	Eastern grey kangaroo (*Macropus giganteus*)	Forbes & Tribe (1970)
79.0	(Sheep)	53.0	Eastern grey kangaroo	Kempton (1972)
91.6	(Sheep)	53.4	Red kangaroo	Hume (1974)
		52.7	Euro (*M. robustus erubescens*)	
62.0	(Sheep)	54.6	Red-necked wallaby (*Macropus rufogriseus*)	Hume (1977a)
		69.2	Red-necked pademelon (*Thylogale thetis*)	
60.3	(Sheep)	56.7	Eastern grey kangaroo	Dellow & Hume (1982a)
		52.7	Red-necked pademelon	
		29.4	Tammar wallaby (*Macropus eugenii*)	
63.0	(Goat)	49.9	Euro	Freudenberger & Hume (1992)
		54.8	Wallaroo (*M. robustus robustus*)	

scaled to 0.64. Herbivorous eutherians generally had higher FMRs than herbivorous marsupials, regardless of body size.

A more recent analysis by Nagy (1994) confirmed a common slope for marsupials of 0.58. Although Green (1997) subsequently proposed different slopes for macropodoid (0.69) and non-macropodoid marsupials (0.52), there is no clear biological basis for lumping all non-macropodoids together, and for this reason the exponent 0.58 is used throughout this book for the purpose of comparing FMRs among marsupials. However, should a more generally acceptable exponent come to light, all tables include sufficient data to enable the reader to recalculate the values on the basis of any other power function.

More useful than FMR for comparative purposes is the ratio of FMR to BMR (calculated by dividing mass-specific FMR by mass-specific BMR) (Koteja 1991). In Nagy's (1987) analysis this ratio decreased with increasing body mass in marsupials, but in eutherians it increased with increasing body mass. The high ratio of FMR to BMR in small marsupials is consistent with their relatively high maintenance energy requirements in captivity (Table 1.2). The high ratio in large eutherians may be partly because most

of the large species in Nagy's (1987) analysis were marine mammals, which have higher costs of thermoregulation in water. When Degen & Kam (1995) analysed data from nine marsupial and 24 eutherian species, none of which was aquatic, FMR:BMR ratios were similar at large body size (5–8 kg). However, at small body size (10–20 g) the ratio in marsupials was still twice that of eutherians.

In Table 1.4 the highest FMR:BMR ratios include those of two small dasyurid species (5.0–6.6) and Leadbeater's possum (6.2). Smith *et al.* (1982) calculated that 73% of the Leadbeater's FMR was attributable to activity and specific dynamic action, consistent with the dispersed nature of its food supply and its well-developed territorial social system. The lowest ratios are from an arboreal folivore, the koala (1.7), and two small wallabies measured during the annual summer drought that is characteristic of their Mediterranean-type environment (1.8–1.9). Similarly, Bradshaw *et al.* (1994) recorded an extremely low FMR:BMR ratio in the golden bandicoot on Barrow Island during an extended drought (1.4), but FMRs trebled after cyclonic rains broke the drought a year later.

1.8 METABOLIC SCOPE

The high FMR:BMR ratio of some small marsupial species raises the question of what is the highest rate of metabolism that can be sustained in the long term? Peterson, Nagy & Diamond (1990) defined *sustained metabolic rates* as time-averaged rates of metabolism in free-ranging animals maintaining body mass over periods that are long enough so that metabolism is fuelled by food intake rather than by transient depletion of energy reserves. Sustained metabolic rate is therefore equivalent to the FMR of animals that are in energy balance. They are less than peak, or burst metabolic rates, which are short term and fuelled largely by anaerobic ATP production from energy stores (mainly glycogen). Peak metabolic rates are limited to no more than one or two minutes because of the toxic effects of lactic acid accumulation, but during that time they may be as much as 100-fold the animal's BMR. In contrast, aerobically fuelled sustained metabolic rates are mostly between 2- and 5-fold BMR (Peterson *et al.* 1990), but can be as low as 1.3 (Karasov 1992) and as high as 7.2 in lactating ground squirrels (Kenagy *et al.* 1990). These multiples of BMR are termed the animal's *sustained metabolic scope.*

Metabolic rates higher than the maximum sustained metabolic rate of a species can be maintained over shorter periods (but for at least several hours) in response to severe cold stress. These rates are fuelled aerobically, but the animal may not be in energy balance, although it must be maintaining a stable body temperature. Such rates have been called *summit metabolic rates* (Gelineo 1964), and the difference between summit metabolic rate and the species' BMR is its *metabolic scope.*

Does a low BMR mean a limited metabolic scope? Dawson & Dawson (1982) compared the metabolic scopes of two small dasyurid marsupials with those of two rodents of similar size when exposed to ambient temperatures as low as −13°C. Summit metabolic rates were similar for the four species, but because BMRs were 30% lower for the marsupials, metabolic scopes for the two marsupials were eight to nine times BMR compared with four to six times BMR for the two eutherians. Dawson & Olson (1988) found that summit metabolic rate in the South American didelphid *Monodelphis domestica* was also eight to nine times BMR. In other words, as Hinds & MacMillen (1986) concluded, marsupials have lower metabolic rates than eutherians within their thermoneutral zone but the same metabolic rates as eutherians below thermoneutrality. Garland, Geiser & Baudinette (1988) then reported that marsupials and eutherians did not differ in maximal running speeds. These two lines of evidence indicate that the numerous consequences of a low BMR do not include restricted thermoregulatory or locomotory responses, and that marsupials have greater metabolic scopes than equivalent eutherians.

1.9 TORPOR AND HIBERNATION IN MARSUPIALS

The very high rates of metabolism required for maintenance of endothermy in small mammals at low ambient temperatures are not sustainable unless food supply is constant in quality and quantity. In the absence of food the internal energy stores deplete in a relatively short time while normothermic, and these small endotherms can save large amounts of energy by abandoning regulation of body temperature at their normal high levels. Heterothermy is particularly common in insectivores, both marsupial and eutherian, because a constant supply of insects is unlikely in the wild, and they cannot ameliorate fluctuations in food availability by caching food as granivores (seed eaters) can.

Heterothermy is manifested in two related but distinct ways; shallow daily torpor and hibernation (deep and prolonged torpor) (Geiser & Ruf 1995). The two states are distinct in terms of average maximum torpor bout duration (11 h in daily torpor versus 355 h in hibernation), mean minimum body temperature (17.4°C versus 5.8°C), minimum metabolic rate (0.54 versus 0.04 mL O_2 g^{-1} body mass h^{-1}), and minimum metabolic rate expressed as a percentage of BMR (30% in daily torpor versus 5% in hibernation).

Among marsupials, daily torpor has been observed in South American didelphid opossums, and Australian dasyurids and small possums from the families Petauridae (sugar glider and Leadbeater's possum) and Tarsipedidae (honey possum) (Table 1.5). Hibernation has been recorded in the South American microbiotheriid *Dromiciops australis* and Australian small possums from the families Burramyidae and Acrobatidae (feathertail

Table 1.4. *Field metabolic rates (FMR) of adult marsupials*

	Cohort	Season	Body mass (g)	Field metabolic rate				Ref.
				mLCO$_2$ g^{-1} h^{-1}	kJ d^{-1}	kJ kg$^{-0.58}$ d^{-1}	$\dfrac{\text{FMR}}{\text{BMR}}$	
Family Didelphidae								
Marmosa robinsoni	A	Sp	28	3.069	53	422	4.7	1
Family Dasyuridae								
Sminthopsis crassicaudata	A	Sp	17	6.720	69	730	6.6	2
Antechinus stuartii	F	W	19	4.290	60	600	4.9	3
	M	W	29	4.150	75	585	4.0	3
	F	W	24	5.188	77	668	5.0	4
	M	W	54	3.525	117	1021	3.4	4
	L	S	29	5.240	94	730	5.0	4
	NL	S	27	4.730	79	640	4.6	4
Antechinus swainsonii	F	B	53	5.292	173	951	—	5
	M	B	73	3.931	177	808	—	5
	A	S	43	2.870	74	460	—	6
	A	W	40	6.740	162	1035	—	6
Phascogale calura	A	W	34	5.350	112	797	—	7
	F	Sp	35	3.360	73	507	—	7
Dasyurus viverrinus	A	S	1029	1.249	793	780	3.2	1
	A	W	1102	1.720	1169	1105	4.4	1
Sarcophilus harrisii	A	S	7900	0.532	2591	781	2.3	1
	A	W	7100	0.660	2890	927	2.9	1
Family Peramelidae								
Isoodon auratus	A	A (Dry)	307	0.447	72	143	1.4	8
	A	A (Wet)	333	1.395	243	460	4.3	8
Isoodon obesulus	A	A	1230	0.908	644	571	2.7	9
Macrotis lagotis	A	S	928	1.225	617	655	3.7	10
	A	W	848	1.033	480	534	3.0	10
	A	S	1132	0.768	455	423	2.5	11
	A	W	1208	0.991	626	561	3.3	11
Family Phascolarctidae								
Phascolarctos cinereus	NL	W	7800	0.503	2050	623	2.4	12
	M	W	10 800	0.358	2030	511	1.7	12
	F	S	5930	0.480	1442	518	1.7	13
	F	W	6078	0.485	1495	532	1.8	13
	NL	Sp	6030	0.570	1748	621	2.4	13
	L	Sp	6730	0.550	1855	624	2.4	13

Table 1.4. (*cont.*)

	Cohort	Season	Body mass (g)	Field metabolic rate				Ref.
				$mLCO_2$ g^{-1} h^{-1}	kJ d^{-1}	kJ $kg^{-0.58}$ d^{-1}	$\dfrac{FMR}{BMR}$	
	M	S	7400	0.383	1470	462	1.5	14
	M	W	7800	0.440	1659	501	1.7	14
Family Petauridae								
Petaurus breviceps	F	Sp	112	2.563	153	545	3.9	15
	M	Sp	135	2.671	192	613	4.1	15
Gymnobelideus leadbeateri	F	Sp	117	3.100	219	760	6.2	16
	M	Sp	133	2.890	232	748	6.1	16
Family Pseudocheiridae								
Pseudocheirus peregrinus	NL		968	1.142	561	572	2.2	17
	L		993	1.515	759	762	2.9	17
	M		994	1.244	643	645	2.5	17
Petauroides volans	F	W	940	1.029	492	512	2.5	18
	M	W	1050	1.024	547	531	2.5	18
Hemibelideus lemuroides	A	Sp	1026	1.293	675	665	—	19
Pseudochirulus herbertensis	A	Sp	1103	0.795	446	421	—	19
Family Tarsipedidae								
Tarsipes rostratus	A	W	10	6.682	34	491	2.7	20
Family Potoroidae								
Potorous tridactylus	F	S	852	1.032	473	519	2.1	21
	M	S	824	0.997	453	507	2.0	21
	F	Sp	757	1.214	512	602	2.6	21
	M	Sp	868	1.337	629	683	2.8	21
Bettongia penicillata	A	S	1100	0.936	524	496	2.4	22
	A	A	1100	1.054	590	558	2.5	22
	A	W	1100	1.242	695	658	3.2	22
Bettongia gaimardi	A	S	1700	1.011	874	642	—	1
Aepyprymnus rufescens	A	S	2860	0.994	1363	741	3.3	23
	A	W	2890	1.011	1495	808	3.4	23
Family Macropodidae								
Lagorchestes hirsutus	A	S	1351	0.753	531	446	—	24
	A	W	1453	0.870	661	532	—	24
Setonix brachyurus	A	S	1900	0.574	548	378	1.8	25
Macropus eugenii	A	S	4380	0.518	1150	488	1.9	25

Table 1.4. (*cont.*)

			Field metabolic rate				
	Cohort	Season	Body mass (g)	mLCO$_2$ g^{-1} h^{-1}	kJ d^{-1}	kJ kg$^{-0.58}$ d^{-1}	$\dfrac{\text{FMR}}{\text{BMR}}$	Ref.
Thylogale billardierii	A	S	5980	0.532	1630	578	2.2	26
Petrogale xanthopus	A	S	8900	0.488	2209	622	2.2	22
Macropus giganteus	M	S	43 900	0.369	8170	911	2.5	26

Note: Cohort: A, adult; F, female; M, male; L, lactating; NL, non-lactating
Season: A, autumn; B, breeding; S, summer; Sp, spring; W, winter
Rate of CO$_2$ production converted to kJ using the equivalents of 25.7kJ per LCO$_2$ for carnivores (Nagy *et al.* 1988), 23.8 for omnivores (Nagy, Bradshaw & Clay 1991) and 21.2 for herbivores (Munks & Green 1995).
FMR/BMR calculated as mass-specific FMR divided by mass-specific BMR (Degen & Kam 1995).
Daily Energy Expenditure (DEE) in kJ d^{-1} converted to a metabolic body mass basis using kg$^{0.58}$ (Nagy 1987, 1994).
References: 1. Green 1997; 2. Nagy *et al.* 1988; 3. Nagy *et al.* 1978; 4. Green *et al.* 1991; 5. Nagy 1987; 6. Green & Crowley 1989; 7. Green, King & Bradley 1989; 8. Bradshaw *et al.* 1994; 9. Nagy, Bradshaw & Clay 1991; 10. Gibson 1999; 11. Southgate, cited by Green 1997; 12. Nagy & Martin 1985; 13. Krockenberger, 1993; 14. Ellis *et al.* 1995; 15. Nagy & Suckling 1985; 16. Smith *et al.* 1982; 17. Munks & Green 1995; 18. Foley *et al.* 1990; 19. Goudberg 1990; 20. Nagy *et al.* 1995; 21. Wallis, Green & Newgrain 1997; 22. Green 1989; 23. Wallis & Green 1992; 24. Lundie-Jenkins, cited by Green 1997; 25. Nagy, Bradley & Morris 1990; 26. Nagy, Sanson & Jacobsen 1990.

glider) (Table 1.5) (Geiser 1994). All but one of these species are either insectivorous or omnivorous, feeding on a mixture of plant exudates and arthropods. The one exception is the honey possum, which feeds only on nectar and pollen (Withers *et al.* 1990). Torpor and hibernation in these various small marsupials is discussed in relation to their nutritional ecology in Chapter 2 (carnivores, including insectivores) and Chapter 3 (omnivores).

1.10 WATER TURNOVER

An animal's requirement for water can be determined by meas uring its rate of water turnover (WTR). If most marsupials have lower BMRs than equivalent eutherians, then it might be expected that water turnover rates in marsupials would also be low, at least when both are measured under standard conditions. For such measurements Nicol (1978) suggested that the ambient temperature should be at the lower end of the animal's thermoneutral zone, since a higher temperature may result in increased water loss for evaporative cooling, while a lower temperature will increase

18

Table 1.5. Torpor and hibernation in marsupials. A more complete list of carnivorous marsupials that enter torpor is given in Table 2.5 (Chapter 2)

Family and species	Body mass (g)	Minimum body temperature (°C)	Torpor duration (h)	Torpor pattern
Didelphidae				
4 species (see Table 2.5)	13–111	16–27	8	Torpor
Microbiotheridae				
Dromiciops australis	30	—	120	Hibernation
Dasyuridae				
18 species (see Table 2.5)	7–1000	11.0–28.2	2–20	Torpor
Myrmecobiidae				
Myrmecobius fasciatus	500	—	—	Torpor
Notoryctidae				
Notoryctes typhlops	60	—	—	Torpor
Petauridae				
Petaurus breviceps	130	15.6	15.5	Torpor
Gymnobelideus leadbeateri	130	—	—	Torpor
Burramyidae				
Cercartetus nanus	21	1.3	552	Hibernation
Cercartetus concinnus	18	4.7	264	Hibernation
Cercartetus lepidus	12	5.9	144	Hibernation
Cercartetus caudatus	30	—	< 24	Hibernation(?)
Burramys parvus	63	2.4	336	Hibernation
Acrobatidae				
Acrobates pygmaeus	12	2	120	Hibernation
Tarsipedidae				
Tarsipes rostratus	10	5	10	Torpor

Source: After Geiser (1994).

metabolic rate and thus increase water turnover. Water must be available *ad libitum*, for water deprivation lowers rates of metabolism and water turnover (Hulbert & Dawson 1974b). Alternatively, food containing a high proportion of water will supply adequate amounts. Water turnover measured under these conditions might then be described as the standard water turnover rate of the species (Nicol 1978).

Water turnover rate can be estimated from the dilution rate of a single dose of tritiated or deuterated water in blood, urine or evaporative water (Rübsamen, Nolda & Engelhardt 1979). If evaporative water is used there will be a small but significant error introduced by the differential movements of hydrogen, tritium and deuterium across membranes (Rübsamen *et al.* 1979). Water turnover rates in free-living animals are routinely measured during measurement of FMR using doubly labelled water.

Using tritiated water, Richmond, Langham & Trujillo (1962) found that the standard water turnover rate in seven species of captive eutherians ranging in size from a 21 g house mouse to a 399 kg horse was 134 ± 32 mL $kg^{-0.80}$ d^{-1}. Denny & Dawson (1975a) subsequently showed that the mean water turnover rate in five macropodid marsupial species under similar conditions was 98 ± 21 mL $kg^{-0.80}$ d^{-1}. Although variation around the mean is considerable in both studies, the macropodid mean is 27% lower than the eutherian mean. These and other values for water turnover rate in captive marsupials are listed in Table 1.6. With few exceptions, the data support the concept of a generally low standard water turnover rate in marsupials. However, Nicol (1978) examined 27 eutherian and 13 marsupial species and concluded that habitat had a far greater effect on standard water turnover rate than did phylogeny. Although the ecological significance of water turnover rates measured under standard conditions is likely to be limited, when compared over a wide range of species it does seem that standard water turnover rates can be useful in separating desert-adapted species from others.

Nagy & Peterson (1988) examined scaling relationships between water turnover rate and body mass across a wide range of animal taxons, both in captivity and in the field. The slope of 0.95 for humans and 96 other eutherians, either captive or domestic, was higher than the slope for 16 captive marsupials (0.77), while the intercept value was lower, making direct comparisons between marsupials and eutherians difficult. Nevertheless, their conclusion was similar to that of Nicol (1978) that habitat and dietary category play major roles in setting a species' standard water turnover rate.

Water turnover rates measured in the field are much more meaningful ecologically. Here, Nagy & Peterson (1988) concluded that mass-corrected water turnover rates were determined much more by dietary habits than by phylogeny. They found a lower slope for free-living marsupials (0.60) than for captive marsupials (0.77), mainly because of the much higher water influx rates of small dasyurids and bandicoots in the field than in captivity, so

Table 1.6. *Water turnover rates (WTR) of captive marsupials with water available* ad libitum

Species	Habitat	Body mass (g)	Water Turnover Rate		Ref.
			mL d^{-1}	mL kg$^{-0.80}$ d^{-1}	
Family Dasyuridae					
Sminthopsis crassicaudata	T-A	15	7.5	216	1
Antechinomys laniger	A	18	6.7	167	2
Dasycercus cristicauda	A	86	11.5	82	3
Dasycercus byrnei	A	127	16.8	88	4
Dasyurus viverrinus	T	1340	162.0	128	5
Sarcophilus harrisii	T	3840	383.0	131	5
	T	5250	393.0	104	6
Family Peramelidae					
Perameles nasuta	T	972	68.3	70	7
Macrotis lagotis	A	1080	48.1	45	7
Isoodon macrourus	T	1470	131.0	96	7
Family Vombatidae					
Lasiorhinus latifrons	A	25 000	433.4	33	8
Family Potoroidae					
Potorous tridactylus	T	1400	137.0	105	9
Family Macropodidae					
Thylogale thetis	T	3520	522.7	191	10
Macropus eugenii	MA	5420	525.7	136	10
	MA	6500	291.0	65	9
Macropus giganteus	T-A	22 100	937.0	79	9
Macropus rufus	A	23 400	1 430.0	115	9
M. robustus erubescens	A	24 100	1 224.0	96	11
M. robustus robustus	T	31 000	1 850.0	119	9

Note: Habitat: A, arid; T, temperate; MA, maritime arid.
References: 1. Morton 1980; 2. Macfarlane 1975; 3. Kennedy & Macfarlane 1971; 4. Haines *et al.* 1974; 5. Green & Eberhard 1979; 6. Nicol 1978; 7. Hulbert & Dawson 1974b; 8. Wells 1973; 9. Denny & Dawson 1975a; 10. Dellow & Hume 1982b; 11. Denny & Dawson 1973.

it is debatable as to whether this exponent should be applied over the whole range of marsupial body masses. When the same data were divided on the basis of diet, analysis of covariance yielded a common slope of 0.71 for 28 herbivores and 23 carnivores, but the latter group had a higher intercept, no doubt because it contained mainly small species. Therefore, with the emphasis in this book on ease of comparison, the data in Table 1.7 on water turnover rates in free-living marsupials are based on an exponent of 0.71.

Table 1.7. *Water turnover rates (WTR) in free-living marsupials*

Species	Cohort	Season	Body mass (g)	WTR mL d^{-1}	WTR mL kg$^{-0.71}$ d^{-1}	Ref.
Family Didelphidae						
Marmosa robinsoni	A	Sp	28	9.4	119	1
Family Dasyuridae						
Sminthopsis crassicaudata	A	S	20	22.4	360	2
	A	W	13	19.8	432	2
	A	Sp	17	13.3	244	3
Antechinus stuartii	A	W	26	13.9	186	4
	NL	S	27	13.2	173	5
	L	S	29	24.9	308	5
Phascogale calura	A	W	34	11.2	123	6
	F	Sp	35	14.0	153	6
Antechinus swainsonii	NL	Sp	47	23.1	202	7
	L	Sp	54	72.5	576	7
	A	S	43	23.4	218	8
	A	W	40	24.5	240	8
Dasyurus viverrinus	A	S	1120	202	186	9
	A	W	920	261	277	9
	L	Sp	984	332	336	9
Sarcophilus harrisii	A	S	7900	724	167	1
	A	W	7100	743	184	1
Family Peramelidae						
Isoodon auratus	A	Au (Dry)	307	27.9	65	10
	A	Au (Wet)	333	47.0	103	10
Isoodon obesulus	F	Au	1060	102	98	11
	M	Au	1370	104	83	11
Isoodon macrourus	A	Au	1410	354	277	12
Macrotis lagotis	A	S	928	73.2	77	13
	A	W	848	66.6	74	13
	A	S	1132	68.0	62	14
	A	W	1208	56.0	49	14
Family Phascolarctidae						
Phascolarctos cinereus	F	Sp	7800	358	83	15
	M	Sp	10 800	475	88	15
	F	S	5930	323	91	16
	F	W	6193	321	88	16
	NL	Sp	5900	248	71	16
	L	Sp	6140	298	82	16

Table 1.7. (*cont.*)

Species	Cohort	Season	Body mass (g)	WTR mL d⁻¹	mL kg⁻⁰·⁷¹ d⁻¹	Ref.
Family Vombatidae						
Lasiorhinus latifrons	A	S	22 200	555	61	17
	A	W	22 200	777	86	17
Family Petauridae						
Petaurus breviceps	F	Sp	112	21.7	103	18
	M	Sp	135	40.6	168	18
Gymnobelideus leadbeateri	F	W	95	44.5	237	19
	M	W	133	42.8	179	19
Family Pseudocheiridae	NL	Sp	968	117	119	20
Pseudocheirus peregrinus	L	Sp	993	158	159	20
	M	S	1046	101	98	20
	M	W	951	124	129	20
Pseudochirulus herbertensis	A	Sp	1103	140	131	21
Petauroides volans	F	W	934	80.4	84	22
	M	W	1042	98.8	92	22
Hemibelideus lemuroides	A	Sp	1026	155	152	21
Family Tarsipedidae						
Tarsipes rostratus	A	W	10	9.1	241	23
Family Phalangeridae						
Trichosurus vulpecula	NL	–	1520	134	100	24
	L	–	1590	163	117	24
Family Potoroidae						
Potorous tridactylus	A	S	816	131	151	25
	A	Sp	784	174	207	25
Bettongia penicillata	A	S	1100	67.1	63	26
Aepyprymnus rufescens	A	S	2850	398	189	26
	A	W	2900	373	175	26
Family Macropodidae						
Setonix brachyurus	A	S	1900	90.5	57	27
Lagorchestes conspicillatus	A	Sp	2230	90.8	51	26
Petrogale inornata	NL	—	3200	251	110	12
Petrogale rothschildi	A	Sp				
		(Dry)	3350	149	63	26
	A	S (Wet)	2740	365	178	26
Macropus eugenii	A	S	4380	270	95	27
Thylogale billardierii	A	S	5980	585	164	28

Table 1.7. (*cont.*)

Species	Cohort	Season	Body mass (g)	WTR mL d^{-1}	WTR mL kg$^{-0.71}$ d^{-1}	Ref.
Petrogale xanthopus	A	S	8900	475	101	26
	A	W (Dry)	8900	497	105	26
	A	W (Wet)	8900	1304	276	26
Macropus rufus	A	S	21 800	861	97	29
M. robustus erubescens	A	S	28 100	1107	104	29
Macropus giganteus	A	S	43 900	2600	177	28

Abbreviations: A, Adult; F, female; M, male; L, lactating; NL, non-lactating
Au, autumn; S, summer; Sp, spring; W, winter.

References: 1. Green 1997; 2. Morton 1980; 3. Nagy *et al.* 1988; 4. Nagy *et al.* 1978; 5. Green *et al.* 1991; 6. Green, King & Bradley 1989; 7. Nagy & Peterson 1988; 8. Green & Crowley 1989; 9. Green & Eberhard 1983; 10. Bradshaw *et al* 1994; 11. Nagy, Bradshaw & Clay 1991; 12. Hulbert & Gordon 1972; 13. Gibson 1999; 14. Southgate, cited by Green 1997; 15. Nagy & Martin 1985; 16. Krockenberger 1993; 17. Wells 1973; 18. Nagy & Suckling 1985; 19. Smith *et al* 1982; 20. Munks & Green 1995; 21. Goudberg 1990; 22. Foley *et al.* 1990; 23. Nagy *et al.* 1995; 24. Kennedy & Heinsohn 1974; 25. Wallis, Green & Newgrain 1997; 26. Green 1989; 27. Nagy, Bradley & Morris 1990; 28. Nagy, Sanson & Jacobsen 1990; 29. Dawson *et al* 1975.

Highest water turnover rates are found in the small carnivorous/insectivorous dasyurids. The range of some of these species extends into the arid zone (e.g. *Sminthopsis crassicaudata*), but their food of animal tissue contains enough water that special measures for water conservation beyond fossoriality and nocturnality are not necessary for survival. Lowest water turnover rates are found in desert-adapted omnivores such as the golden bandicoot and herbivores, including the spectacled hare-wallaby and Rothschild's rock-wallaby. Low water turnover rates are also seen in Mediterranean-zone species at the end of the long annual summer drought; examples in Table 1.7 include the omnivorous southern brown bandicoot and the herbivorous small wallabies *Setonix brachyurus* (quokka) on Rottnest Island and *Macropus eugenii* (tammar wallaby) on Garden Island near Fremantle, Western Australia. Low water turnover rates are also characteristic of the strictly arboreal folivores *Phascolarctos cinereus* (koala) and *Petauroides volans* (greater glider).

Water use increases when more water becomes available, either directly or indirectly, because metabolic rates increase as more food also becomes available and is processed by the animal; three examples (one bandicoot and two rock-wallabies) in Table 1.7 illustrate this. Other factors that increase metabolic rate also increase WTR. Thus WTRs tend to be higher in males than in non-lactating females (males generally have higher meta-

bolic rates), and higher in winter (increased thermoregulatory demands) than in summer. The largest increases in WTRs are generally seen in females during lactation, when there are significant increases in both metabolic rate and excretion of water in milk.

1.11 PROTEIN TURNOVER AND NITROGEN REQUIREMENTS

One of the major components of BMR is protein synthesis and degradation in the body. The energy costs directly involved in whole-body protein synthesis, together with other processes associated with protein synthesis, such as RNA turnover, amino acid activation and intermediary metabolism, account for a significant fraction of an animal's BMR (Reeds, Fuller & Nicholson 1985). Thus there should be a close relationship between BMR and rates of whole-body protein synthesis. This indeed appears to be so. White, Hume & Nolan (1988) found that protein turnover rates in three wallabies, the tammar, parma wallaby (*M. parma*) and red-necked pademelon (*Thylogale thetis*) were 23-47% lower than those reported in six eutherian species by Waterlow (1984), in line with the generally lower BMRs of macropodid marsupials. Wombats (Chapter 4) have even lower BMRs and protein turnover rates that are 57–74% lower than Waterlow's (1984) eutherian values (Barboza, Hume & Nolan 1993).

Among the wallabies, whole-body protein synthesis rates were significantly lower in the tammar than in the other two species (White *et al.* 1988), in line with a lower fed (but not basal) metabolic rate and a lower maintenance energy requirement (Table 1.2).

Differences in protein turnover rates are manifested in the whole animal in differences in rates of inevitable loss of nitrogen, mainly in the faeces (as metabolic faecal nitrogen) and urine (as endogenous urinary nitrogen). Metabolic faecal nitrogen and endogenous utinary nitrogen account for the bulk of an animal's maintenance nitrogen requirement. Maintenance nitrogen requirements are measured in captive animals fed a range of diets that ideally vary only in their content of protein, or nitrogen. The maintenance nitrogen requirement of the species is then the nitrogen intake that leads to zero nitrogen balance, where nitrogen balance is the difference between nitrogen intake and nitrogen excretion (urine plus faeces). Other avenues of nitrogen loss from the body, such as shed hair and sloughed skin, are negligible and usually ignored.

Importantly, compared to energy, the total requirement for nitrogen is much less affected by additional requirements for free existence such as activity and thermoregulation. Thus estimates of the maintenance requirement of captive animals for nitrogen are likely to be a realistic reflection of the needs of adult animals in the wild. Only growth and reproduction impose significant increments on the total protein requirement (Fig 1.4),
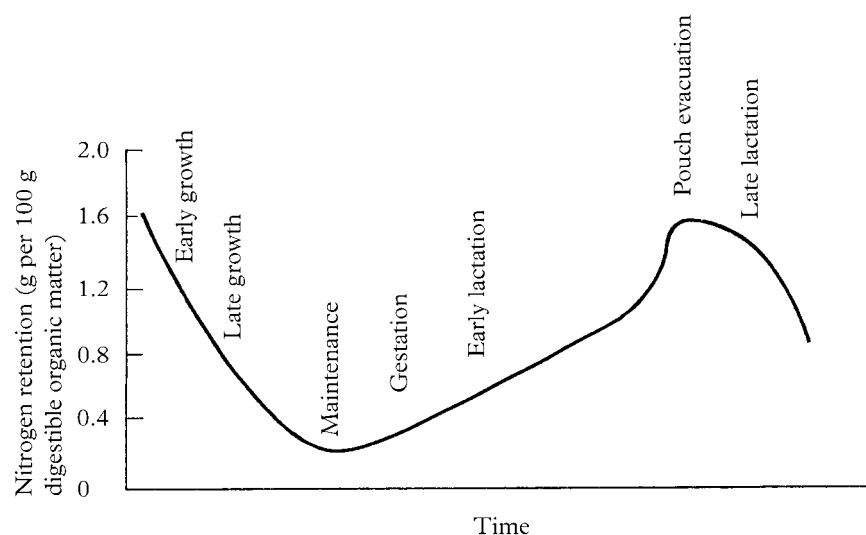
Figure 1.4 Total protein requirement of a female marsupial, measured as the ratio of nitrogen retention to digestible organic matter intake. Although the curve is adapted from a ruminant model, it is probably applicable to all therian mammals, even though the relative lengths of gestation and lactation differ between marsupials and eutherians; in marsupials gestation is short and its protein requirement is low, but lactation is extended and expensive in terms of both protein and energy.

but protein requirements for these physiological functions in marsupials have not been investigated to any extent. Wallis & Hume (1992) found that total nitrogen requirements of breeding female *Aepyprymnus rufescens* (rufous rat-kangaroos or rufous bettongs) at peak lactation were four times those of adult male animals.

Maintenance nitrogen requirements that have been established for marsupials are listed in Table 1.8. Values are given for both dietary and truly digestible nitrogen. Dietary requirements depend on several factors, among them differences in digestibility of the nitrogen in the diet. Truly digestible requirements at least partially allow for such differences. Most estimates of the maintenance requirement for truly digestible nitrogen of terrestrial herbivorous marsupials seem to be within the range 150–250 mg $kg^{-0.75}$ d^{-1}. In contrast, many equivalent eutherians have requirements calculated on the same basis that are twice these levels (Robbins 1983). Thus it seems that the basic phylogenetic difference seen in BMR between marsupial and eutherian grazer/browsers is reflected also in maintenance nitrogen requirements.

Moreover, just as with BMRs, diet and habitat also seem to play a role in shaping maintenance nitrogen requirements. Habitat effects are clearly seen among the Macropodidae, with the highest requirements associated with moist forest habitats in the case of the red-necked pademelon and

26

parma wallaby and the lowest with the arid-zone euro. Diet effects are demonstrated by the data for the arboreal folivores. Common brushtail possums (*Trichosurus vulpecula*) maintained on *Eucalyptus melliodora* (yellow box) foliage required more than twice the amount of nitrogen as on a semi-purified diet containing no plant secondary metabolites (PSMs). Plant secondary metabolites are compounds synthesised for purposes other than general metabolism, such as for defence against invasion by pathogens or ingestion by herbivores. The main plant secondary metabolites found in eucalypt foliage are phenolics and terpenes (essential oils). Their anti-herbivore effects are discussed in Chapter 5. The dry matter of *E. melliodora* foliage contains about 26% of total phenolics, which resulted in large losses of non-dietary faecal nitrogen (largely microbial cells) (Foley & Hume 1987b). The reason for the high maintenance requirement of greater gliders fed *E. radiata* (narrow-leafed peppermint) foliage is probably the high content (11%) of terpenes in this species. In this case there were unusually high losses of nitrogen in the urine, mainly as ammonium ions because of the large amount of glucuronides excreted as conjugates of terpenes, and the need to maintain the acid–base balance of the animal (Foley 1992). The mechanism involved is treated in greater detail in Chapter 5.

The only non-herbivores in Table 1.8 are the didelphid *Caluromys philander*, the eastern pygmy-possum (*Cercartetus nanus*) and the sugar glider (*Petaurus breviceps*). *C. philander* feeds mainly on fruit but also nectar, gums and invertebrates (see Chapter 3), and its maintenance nitrogen requirements are relatively low. The sugar glider feeds on a mixture of *Acacia* gum, eucalypt sap and insects. Its low maintenance dietary nitrogen requirement of 87 mg $kg^{-0.75}$ d^{-1} is partly explained by an unusually low loss of metabolic faecal nitrogen (0.7 mg g^{-1} dry matter intake) compared with an average value in herbivorous marsupials of 2.8 (Smith & Green 1987). Metabolic faecal nitrogen is a mixture of undigested bacteria containing nitrogen of endogenous origin, abraided gut mucosal cells and unabsorbed digestive enzymes. The absence of indigestible fibre in the diets of the three non-herbivores would minimise bacterial growth and gut abrasion, and thus metabolic faecal nitrogen.

Endogenous urinary nitrogen (EUN) loss was also low in the sugar gliders (25 mg $kg^{-0.75}$ d^{-1}) compared with an average value in macropod marsupials of 54, although euros average 32 mg $kg^{-0.75}$ d^{-1} (see Table 1.9). Common wombats also have low EUN losses (31 mg $kg^{-0.75}$ d^{-1}). Endogenous urinary nitrogen is related more closely to the animal's metabolic rate than to any aspect of its protein metabolism. In eutherians, Smuts (1935) has shown that about 2 mg of EUN is excreted for each kcal of basal heat production. Assuming that a similar relationship holds in marsupials, EUN should be lower in macropod marsupials than in equivalent eutherians. The data in Table 1.9 demonstrate that this is so; the average value for

Table 1.8. Maintenance nitrogen requirements of marsupials. All data in mg N kg$^{-0.75}$ d^{-1}

Species	Body mass (kg)	Diet	Maintenance requirement		Ref.
			Dietary	Truly digestible	
Family Didelphidae					
Caluromys philander	0.43	Fruit, casein	176	146	1
Family Phascolarctidae					
Phascolarctos cinereus	5.1–8.3	Eucalypt foliage	283	271	2
Family Vombatidae					
Vombatus ursinus	27.9	Chopped oat straw, grain	158	71	3
Lasiorhinus latifrons	23.1	Chopped oat straw, grain	201	116	3
	29.0–31.0	Chopped oat straw, grain	205	—	4
Family Burramyidae					
Cercartetus nanus	24	Pollen	46	43	5
	24	Mealworms	147	127	5
Family Petauridae					
Petaurus breviceps	0.15	Honey, pollen	87	—	6
Family Pseudocheiridae					
Pseudocheirus peregrinus	0.6–0.7	Eucalypt foliage	380	290	7
Petauroides volans	1.1	Eucalypt foliage	700	560	8

Family Phalangeridae					
Trichosurus vulpecula	1.3–2.5	Semi-purified	203	189	9
	2.5	Eucalypt foliage	560	420	8
Family Potoroidae					
Potorous tridactylus	0.9	Grain-based	—	199	10
Bettongia penicillata	1.1	Grain-based	—	199	10
Aepyprymnus rufescens	2.8–3.1	Grain-based	—	199	10
Family Macropodidae					
Thylogale thetis	3.8–4.8	Chopped alfalfa, sucrose	600	530	11
Macropus parma	3.7–3.9	Chopped alfalfa, sucrose	566	477	12
Macropus eugenii	4.2–5.4	Chopped oat hay, casein	290	250	13
	3.8–5.1	Chopped alfalfa, sucrose	240	230	11
M. robustus robustus	11.8–17.7	Chopped oat hay, casein	300	240	14
M. r. erubescens	10.5–15.6	Chopped oat hay, casein	290	160	15
M. giganteus	18.6–30.3	Chopped oat hay, casein	350	270	14

References: 1. Foley, Charles-Dominique & Julien-Laferriere 1999; 2. Cork 1986; 3. Barboza, Hume & Nolan 1993; 4. Wells, 1968; 5. van Tets 1996; 6. Smith & Green 1987; 7. Chilcott & Hume 1984b; 8. Foley & Hume 1987b; 9. Wellard & Hume 1981b; 10. Wallis & Hume 1992; 11. Hume, 1977b; 12. Hume 1986; 13. Barker 1968; 14. Foley, Hume & Taylor 1980; 15. Brown & Main 1967.

Table 1.9. *Endogenous urinary nitrogen (EUN) in seven marsupial and five eutherian herbivores*

Species	Body mass kg	EUN mg kg $^{-0.75}$ d^{-1}	Ref.
Marsupials			
Quokka (*Setonix brachyurus*)	2.0–3.6	43	Brown (1968)
Black-footed rock-wallaby (*Petrogale lateralis*)	3.9	49	Brown (1968)
Tammar wallaby (*Macropus eugenii*)	4.2–5.3	58	Barker (1968)
Euro (*M. robustus erubescens*)	8.5–19.7	32	Brown (1968)
Red kangaroo (*M. rufus*)	14.4	87	Brown (1968)
Hairy-nosed wombat (*Lasiorhinus latifrons*)	23.1	42	Barboza *et al.* (1993)
Common wombat (*Vombatus ursinus*)	27.9	31	Barboza *et al.* (1993)
Eutherians			
Guinea pig (*Cavia porcellus*)	0.3–0.5	145	Brody (1945)
Rabbit (*Oryctolagus cuniculus*)	1.2–2.8	148	Brody (1945)
Goat (*Capra hircus*)	24.2–62.0	115	Hutchinson & Morris (1936)
Sheep (*Ovis aries*)	31.8–42.0	87	Smuts & Marais (1938)
Camel (*Camelus dromedarius*)	250	60	Schmidt-Nielsen *et al.* (1967)

five macropods is less than half that for five herbivorous eutherians. Note-worthy, however, is the camel which overlaps the marsupial range; its BMR is also substantially below the Kleiber (1961) prediction for eutherians (Schmidt-Nielsen *et al.* 1967).

A similar argument cannot be used to explain the unusually low EUN of sugar gliders, because their BMR is within the macropod range (Table 1.1). An alternative explanation is that part of their endogenous nitrogen is retained by being recycled to the digestive tract. Herbivores excrete less urea, one component of EUN, than non-herbivores, because of recycling of endogenous urea to their gut, where resident microorganisms rapidly de-grade it and use a portion of the ammonia released for the synthesis of their own protein. The amount of ammonia trapped in this way depends on the energy available to the microbes. Although the sugar glider is an omnivore, the gums on which it feeds may be largely fermented in the hindgut. The caecum of the sugar glider is surprisingly large for an omnivore (see Chap-ter 3), which supports this view. Their high-energy diet may be expected to result in efficient trapping of recycled nitrogen, resulting in lower urea excretion rates than those of herbivores feeding on lower-energy plant material. This would lower their EUN.

Another major component of EUN is creatinine. Creatinine is a meta-

bolic end-product of creatine, a precursor of the high-energy compound phosphocreatine found in muscle. Creatine is synthesised in the liver. Surplus creatine from the reversible interconversion of creatine and phosphocreatine in muscle is converted to creatinine and excreted by the kidneys. The rate of creatinine excretion by a healthy animal fed diets free of creatine and creatinine (as those of herbivores are) appears to be equivalent to the rate of creatine synthesis in the liver, which proceeds at a rate proportional to BMR. Unlike urea, an end-product of nitrogen metabolism, creatinine does not appear to enter the digestive tract to be degraded by microorganisms. Nor does its rate of excretion appear to be affected by muscular activity or other factors that increase metabolic rate, although it is disturbed by anything that raises deep body temperature (Mitchell 1962).

Thus in healthy herbivores any differences in the rate of creatinine excretion should reflect differences in BMR. Table 1.10 presents data on creatinine excretion from seven marsupial and five eutherian herbivores. Although variation around the mean values for some species is high, it does appear that, in general, marsupial levels are below those of the eutherians listed, consistent with their lower BMR. Among the marsupials it is of interest that the euro is the lowest and the red-necked pademelon is among the highest in terms of both creatinine excretion rate and maintenance nitrogen requirement. Thus there are several links between nitrogen and energy metabolism.

1.12 OTHER NUTRIENTS

Relative to energy, water and protein, there is only limited information on the requirements of marsupials for the micronutrients (vitamins, minerals and essential fatty acids). There is no evidence of unusually high requirements for any micronutrient among the marsupials, but there are suggestions that several micronutrients are required by some marsupials in extremely small amounts. An example is provided by quokkas on Rottnest Island. Early attempts to graze sheep on the island failed when the sheep suffered from deficiencies of several trace elements, including copper and cobalt. In contrast, studies by Barker (1960, 1961a, b) found no evidence of deficiencies of either mineral in quokkas on Rottnest, despite the poor mineral status of the sandy, limestone-derived soils. Requirements for the two minerals by the quokkas were calculated to be less than 50% of the requirements of sheep (see Chapter 7), resulting in a much wider nutritional niche for the native herbivore.

Another example is provided by the low ash content of *Eucalyptus* foliage (see Fig. 5.1), suggestive of a low mineral status. The absence of any reports of mineral deficiencies in koalas and greater gliders, two arboreal marsupials that feed almost exclusively on eucalypt leaves (Chapter 5), provides indirect evidence that mineral requirements of these two folivores are also

Table 1.10. Creatinine excretion in seven marsupial and *five* eutherian species

Species	Body mass (kg)	Creatinine excretion (mg kg $^{-0.75}$ d^{-1})	Ref.
Marsupials			
Long-nosed potoroo (Potorous tridactylus)	1.2	41	Nicol (1976)
Quokka (Setonix brachyurus)	3.3	34	Ramsay (1966); Kinnear & Main (1969)
Tammar wallaby (Macropus eugenii)	2.4–5.9	29	Fraser & Kinnear (1969)
	3.8	30	Wilkinson (1979)
	4.3	24	Wilkinson (1979)
Red-necked pademelon (Thylogale thetis)	4.3	39	Fraser & Kinnear (1969)
Euro (M. robustus erubescens)	14.6	24	Barboza et al. (1993)
Hairy-nosed wombat (Lasiorhinus latifrons)	23	36	Barboza et al. (1993)
Common wombat (Vombatus ursinus)	28	25	
Eutherians			
Rabbit (Oryctolagus cuniculus)	2.0	55	Brody (1945)
Pig (Sus scrofa)	24–79	56	Smuts (1935)
Sheep (Ovis aries)	37–50	62	Fraser & Kinnear (1969)
Cow (Bos taurus)	322	110	Brody (1945)
Camel (Camelus dromedarius)	515	85	Brody (1945)

low. Similarly, Ullrey, Robinson & Whetter (1981a) reported concentrations of phosphorus, sodium, selenium, zinc and copper in eucalypt foliage consumed by koalas at San Diego Zoo which would have been inadequate for sheep or horses.

A report by Barboza & Vanselow (1990) on copper toxicity in a southern hairy-nosed wombat (*Lasiorhinus latifrons*) maintained in captivity on formulated diets containing a commercial supplement designed for growing pigs also suggests that the mineral requirements of wombats may be much lower than those of domestic animals.

Although largely anecdotal, these examples indicate that the marsupial–eutherian differences in energy, water and protein requirements discussed earlier in this chapter may well apply also to the micronutrients. Not much more can be said though until more direct comparisons between marsupials and equivalent eutherians are conducted.

1.13 SUMMARY AND CONCLUSIONS

The concept of the nutritional niche of an organism was introduced in this chapter to set the framework for the rest of the book. The nutritional niche of a species can be defined principally by what it needs in terms of energy and specific nutrients, and how it harvests and extracts those needed nutrients from the food resources available. In general, more generalist feeders have wider nutritional niches than specialists; for example, species that feed on fruit and leaves have wider nutritional niches than specialist folivores. The amount of any particular nutrient required has two components: the amount needed for maintenance of the adult animal, and additional amounts needed for growth, reproduction and free existence. Maintenance requirements are often closely related to the species' basal metabolic rate, but the extent to which requirements are increased above maintenance in different physiological states and by environmental factors is dependent on many factors. Sound knowledge of the basic biology and ecology of the species is necessary before the likely relative importance of these various physiological and environmental factors can be appreciated. This applies particularly to the total energy and thus total food requirements of free-living animals. Information from captive animals studied under controlled conditions is vital for describing and understanding mechanisms. Information from free-living animals in different seasons, different physiological states and different environments is equally vital for interpreting captive results and for testing extrapolations from captivity to the wild state.

There is now enough information from captive and field studies to suggest that basal metabolic rates of marsupials have a phylogenetic base that is modified in many cases by food habits and activity levels. Generally though, marsupials have lower BMRs than their eutherian counterparts.

This trend is often reflected in lower maintenance requirements for energy, protein and water, but at the level of FMRs marsupial–eutherian comparisons are limited by insufficient data. Nevertheless, it appears that summit metabolic rates of small marsupials are similar to those of small eutherians, and thus small marsupials have greater metabolic scopes. Greater metabolic scopes in marsupials mean that a low basal metabolic rate does not translate into limited capacity for thermoregulation or locomotory responses. However, in inadequate environments a low BMR serves to maximise the life of energy stores.

A generally low standard water turnover rate in captive marsupials cannot be translated easily into relative field requirements because of the different scaling relationships associated with marsupials and eutherians. However, it is clear that phylogeny plays a subordinate role to environment in determining total water requirements in free-living marsupials and eutherians.

Less information is available on nitrogen requirements, but in this case maintenance requirements determined in captivity are more directly applicable to the free-living animal. What is needed is more information on the addition costs of growth and reproduction of a range of marsupial species. The next seven chapters deal with the ways in which the various groups of marsupials satisfy their energy and other nutrient requirements from different foods. The groups are separated by their food habits and mode of digestion, beginning with the carnivores.