Cambridge University Press
978-0-521-59555-1 - Marsupial Nutrition
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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

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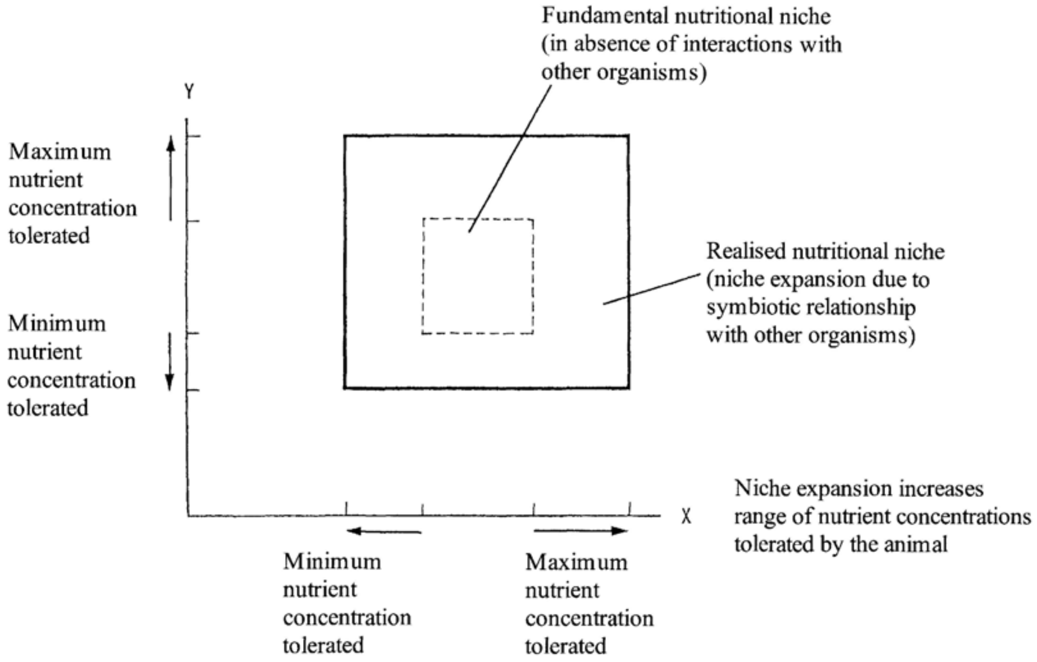

Figure 1.1 The fundamental and realised nutritional niche of an animal, showing the concept of niche expansion due to symbiotic relationship with other organisms. Adapted from Kinnear *et al.* (1979).

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-

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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

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shown to vary with body mass according to the equation $\text{BMR} = a\ \text{Mass}^{b}$. 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. $\text{Mass}^{0.67}$), 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 $\text{kg}^{-0.75}\ \text{d}^{-1}$, 293 if the BMR is in kJ $\text{kg}^{-0.75}\ \text{d}^{-1}$, or 3.34 if the BMR is in the SI (Système International d'Unités) units of Watts $\text{kg}^{-0.75}$.

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)	BMR				Ref.
		mLO$_2$ g^{-1} h^{-1} [a]	kJ kg$^{-0.75}$ d^{-1} [b]	W kg$^{-0.75}$ [c]	% [d]	
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

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Table 1.1. *cont.*

Species	Body mass (g)	BMR mLO$_2$ g^{-1} h$^{-1\,a}$	BMR kJ kg$^{-0.75}$ d$^{-1\,b}$	BMR W kg$^{-0.75c}$	%^{d}	Ref.
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 mLO$_2$ g^{-1} h^{-1} ^{a}	BMR kJ kg$^{-0.75}$ d^{-1} ^{b}	BMR W kg$^{-0.75c}$	%^{d}	Ref.
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

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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)

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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 $\mathrm{kJ\,kg^{-0.75}\,d^{-1}}$, 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