

Basal Metabolic Rates in Mammals: Allometry, Phylogeny and Ecology

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Basal metabolic rates in mammals: allometry, phylogeny and ecology

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Abstract. Basal metabolic rate in mammals increases allometrically with body weight, irrespective of the taxonomic level chosen for analysis. Species' deviations from the allometric curve (relative basal metabolic rates) are associated with differences in diet, habitat and taxonomic affinity. When correlations with taxonomy are controlled for, the only consistently significant association that remains is the higher relative basal metabolic rates of vertebrate eaters.

Key-words: Basal metabolic rates, diet and habitat, mammals, comparative studies

Introduction

Interspecific comparisons demonstrate that mammalian metabolic rates increase with body weight, even under conditions of controlled activity and temperature. Kleiber (1932) and Brody & Proctor (1932) were the first to note that basal metabolic rates are proportional to the 0·75 power of body weight. Why the allometric exponent should take this particular value is unclear (but see McMahon, 1973, 1975; Calder, 1984). However, the allometric relationship is not perfect, and some taxa have appreciably different basal metabolic rates from those expected by their body weights (Hayssen & Lacy, 1985). Recently, attention has been given to explaining such deviations.

McNab (1980, 1983, 1986a,b) has argued that diet and habitat are important determinants of basal metabolic rates among eutherian mammals. Species feeding on vertebrates, herbs and nuts generally have higher basal metabolic rates for their weight (such species are referred to as having high relative basal metabolic rates) than those that feed on invertebrates, fruit and the leaves of woody plants (McNab, 1986a). In addition, moderately sized species that are predominantly arboreal have lower relative basal metabolic rates than similarly sized terrestrial species that forage on the same kind of food (McNab, 1986a). This association

between basal rate and diet is regarded by McNab as 'causative, in the sense that various properties of the foods may limit the rate at which energy is acquired by a mammal, and therefore the rate at which the mammal can expend energy' (McNab, 1986a, p.7). In attempting to explain these associations, McNab argues that mammals other than marsupials (see McNab, 1986b) exhibit the highest possible metabolic rates that their ecological and physiological requirements will allow, since higher rates yield higher reproductive output.

However, many of McNab's ecological correlates of relative metabolic rates may also be taxonomic associations. For example, species from the order Carnivora generally eat vertebrates while most primates feed on invertebrates, fruit and the leaves of woody plants. If carnivores have higher relative basal metabolic rates than do primates, and if there were many carnivores and primates in his sample, the associations McNab (1986a) described could result from a difference in relative metabolic rates between species from the two orders. Such differences in diet and metabolic rate could have arisen in the distant past and have been retained by inertia, rather than arising from evolutionary convergence (see Harvey & Mace, 1982; Ridley, 1983). Furthermore, there are many other differences between primates and carnivores in addition to diet, for example in life-history patterns. Any difference in relative basal metabolic rate between the two groups could be more closely associated with differences in life history than diet, in which case taxonomic affinity would merely stand as a surrogate for some other directly relevant variable. The comparison between primates and carnivores is illustrative rather than substantive, but we believe that statistical procedures can and should be used to help reveal possible taxonomic effects. This paper attempts to identify ecological and taxonomic correlates of relative basal metabolic rate among mammals.

Methods

Body weight, metabolic rate and diet

The basal metabolic rates and body weights of 265

M. A. Elgar & P. H. Harvey species of mammals from 18 orders were extracted from the literature. Data and sources are given in the Appendix. Corbet & Hill's (1980) taxonomy has been followed (except that the Tupaiidae have been included within the Insectivora). In order to avoid statistical problems that might arise from comparing a variable (body weight) with a mathematical function of itself (metabolic rate divided by body weight), total basal metabolic rate was used for the analyses (measured as oxygen consumption per hour) rather than mass specific basal metabolic rate (which was used by McNab, 1986a).

Following McNab (1986a), each species was assigned to one of 10 diet categories (roots or tubers, grass, leaves, fruit, nuts or seeds, pollen, invertebrates, vertebrates, blood, and omnivorous) and one of four habitat categories (terrestrial, arboreal, aquatic and fossorial). Species in the same genus always had the same diet and habitat.

Analysis

Body weight and basal metabolic rate were logarithmically transformed before data manipulation and analysis. Nested analyses of variance were used to determine the taxonomic distribution of the variance in both body weight and basal metabolic rate, which according to Harvey & Clutton-Brock (1985) can indicate an appropriate level for statistical analysis. Analysis at lower taxonomic levels could spuriously increase the sample size, while analysis at higher levels would ignore appreciable amounts of variation in the original data set and unnecessarily reduce the sample size.

We tested for changes in the allometric exponent relating metabolic rate to body weight at each taxonomic level, by using average values of metabolic rate and body weight at successive taxonomic levels. Generic points were means of constituent species values. Higher-level estimates were calculated hierarchically from mean values at the lower levels. Major axis and conventional regression slopes (Sokal & Rohlf, 1981) were calculated for each taxon in which the number of subtaxa for which data were available exceeded two. For example, slopes were calculated only for those families with three or more genera. A 'common' major axis was then estimated as the sample-size-weighted mean of all the slopes at each taxonomic level. Our statistical protocol is similar to that used by Martin & Harvey (1985) in their analysis of brain-size allometry.

Deviations orthogonal to the slope of the major axis lines of log basal metabolic rate on log body weight were calculated and used as measures of relative metabolic rates.

Results

Basal metabolic rate and body weight

The allometric exponents relating basal metabolic rate to body weight (measured as major axis and conventional regression analysis slopes) for different taxonomic levels are given in Table 1. About 80% of the variation in both basal metabolic rate and body weight was found among orders within the class (see Table 2). That is, species

Table 1. Changes in allometric exponent between body weight and metabolic rate for different taxonomic levels, together with 95% confidence limits (CL).

Taxonomic level	df	Common correlation	Common major-axis (95% CL)	Common regression (95% CL)
Among orders within mammals	15	0.98	0.83 (0.76-0.92)	0.82 (0.74-0.90)
Among families within orders	47	0.96	0.73 (0.67-0.80)	0.71 (0.64-0.78)
Among genera within families	102	0.95	0.75 (0.70 - 0.80)	0.72 (0.67 - 0.77)
Among species within genera	53	0.80	0.73 (0.57-0.91)	0.60 (0.46-0.74)

Table 2. Distribution of variance in body weight, basal metabolic rate (BMR) and relative metabolic rate at different taxonomic levels. Percentage variance refers to the additional variance located at that taxonomic level. The method used is described by Sokal & Rohlf (1981). The zero values indicate that there was the same (or less) variance among generic values within families than among species values within genera.

		Percentage variance					
Taxonomic level	df	BMR Body weight		Relative BMR			
Among orders within mammals	17	81.84	80.65	43.40			
Among families within orders	52	13.54	15.85	21.71			
Among genera within families	122	0.00	0.00	0.00			
Among species within genera	73	4.62	3.50	34.89			

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in mammals

within genera, genera within families and families within orders varied relatively little on both measures. The order-level plot with its associated 0.83 exponent was therefore chosen as the base plot for relating metabolic rates to body weights (see Fig. 1).

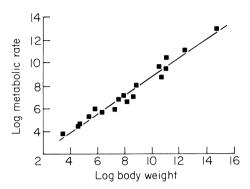


Fig. 1. The relationship between metabolic rate and body weight for different orders of mammals (order values calculated as described in text). Nested analysis of variance (see Table 2) indicated that this is the appropriate level of analysis.

Basal metabolic rate, diet and habitat

The deviations of order values from the line of log metabolic rates on log body weight enable comparison of variation in metabolic rates, because differences in body weight have been accounted for. Positive deviations indicate that members of an order tend to have higher metabolic rates than would be expected for a 'typical' order of the same body weight, while negative deviations indicate that they have lower metabolic rates than expected. These deviations (which we refer to as 'relative metabolic rates') can then be correlated with either diet or habitat.

In order to compare our approach with the results described by McNab (1986a), relative basal metabolic rate was compared with diet at the species level (that is using species' deviations from the major axis line for the whole class set across species points). One-way analyses of variance revealed significant heterogeneity ($F_{9,281} = 7.28$, P< 0.001): species that feed on grass or vertebrates tend to have higher relative metabolic rates than species feeding on invertebrates, roots or leaves. The same analysis for habitat also revealed significant heterogeneity ($F_{3,281} = 5.27$, P < 0.01): aquatic species tend to have higher metabolic rates than fossorial species. The results of these analyses at the species level are comparable with McNab's (1986a).

If the differences in relative metabolic rate are directly associated with ecological variables, then

the patterns of variation should be found across taxonomic categories, such as orders. However, several orders contain families characterized by different diets and habitats (which we refer to as polytypic orders), and even some families are polytypic. In our sample, species within genera always have the same diet and habitats. In searching for taxon-independent ecological correlates of relative basal metabolic rates, it seems sensible to use monotypic order values as independent points for analysis. But how should polytypic orders be dealt with? Over one-half of the variation in relative metabolic rate is found below the order level (see Table 2). Extreme alternatives are (A) to calculate a single value for each diet or habitat category represented in each order, and to use these as independent data points, or (B) to use the highest taxonomic non-variable category as an independent datum point for analysis. For example, if an order contains two families, and the members of one are all herbivores while the other contains both herbivores and frugivores, under alternative A the order would contain just two independent points for analysis (one herbivore, one frugivore), while under alternative B there would be three points (two herbivore, one frugivore). If there were a complete phylogeny, one possible approach would be to decide between alternatives A and B according to the phylogeny (following Ridley, 1983); if herbivory was the diet in the most recent common ancestor, then alternative A would be chosen, whereas if frugivory was the ancestral diet, herbivory would have evolved at least twice and alternative B would be chosen.

The average relative basal metabolic rates for different diet and habitat categories within each order (calculated as under alternative A) are presented in Figs 2 and 3. Are some diet or habitat categories consistently associated with relatively high or relatively low basal metabolic rates after accounting for taxonomic effects? Standard statistical procedures cannot easily answer that question because of the unequal representation of diet and habitat categories among orders. In our search for pattern in Figs 2 and 3, we have performed a series of simulation studies that randomize relative metabolic rates, and habitat and diet categories subject to particular constraints. The simulated results were then compared with the original data.

First, the procedure for diet under alternative A is described to illustrate how our simulation tests were constructed:

(1) The average relative metabolic rate was

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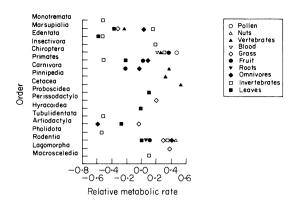


Fig. 2. The relative metabolic rates for different diet categories within 18 orders of mammals. The key shows ascending values of relative metabolic rate, with pollen high and leaves low (see text for details).

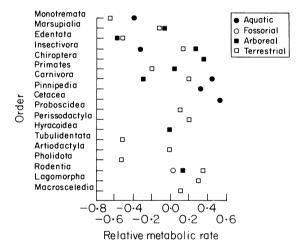


Fig. 3. The relative metabolic rates for different habitat categories within 18 orders of mammals. The key shows ascending values of relative metabolic rate, with aquatic high and terrestrial low (see text for details).

calculated for each of the 18 orders as the mean of the constituent points for a given diet on Fig. 2.

- (2) These average order values were then randomly reassigned among the orders, so that perhaps Carnivora was given the value for Edentata.
- (3) For each order containing more than one diet category, the deviations from the original order mean were calculated. These deviations were then randomly reassigned among groups within each order. For example, frugivorous primates had relative basal metabolic rates that were 0·19 above the primate mean, whereas the value for leafeating primates was 0·06 below the primate mean. In the reassignment, these values might be swapped, allotted to other diet categories within the primate order, or retain their original values.
- (4) A new, simulated relative metabolic rate for each diet category in each order was calculated as the sum of the new order value and the new diet value within the order.
- (5) The sum of the simulated relative metabolic needs for each diet category was calculated and compared with the sum calculated from the actual data given in Fig. 2.
- (6) Procedures 1–5 were repeated 2000 times. Thus, the simulations generate a distribution of relative metabolic rate effects that would be obtained for diet and habitat if these ecological variables were not confounded with taxonomy. The number of occasions out of 2000 that the observed summed relative metabolic needs were greater or less than the simulated summed relative metabolic needs for each diet category are given in Table 3.

The simulation showed that relative metabolic rates of vertebrate eaters tend to be higher (P = 0.03) and invertebrate eaters lower (P = 0.03) than expected from the random patterns derived by the

Table 3. The proportion of times an actual diet or habitat category value was less than that derived from a simulation model. Simulations were repeated 2000 times (see text for details of procedure). Vertebrate eaters have higher and invertebrate eaters have lower relative metabolic rates.

	Simulation			Simulation		
Diet	A	В	Habitat	A	В	
Vertebrates	0.029	0.031	Terrestrial	0.947	0.441	
Grass	0.204	0.375	Arboreal	0.571	0.430	
Seeds/nuts	0.095	0.073	Aquatic	0.213	0.272	
Pollen	0.063	0.052	Fossorial	0.490	0.588	
Fruit	0.288	0.358				
Omnivorous	0.527	0.278				
Leaves	0.910	0.928				
Invertebrates	0.974	0.887				
Blood	0.263	0.283				
Roots	0.428	0.516				

Relative metabolic rates in mammals simulation (Table 3). An equivalent set of simulations was performed on the habitat data. This simulation failed to reveal any significant patterns.

The procedure for the simulation under alternative B was similar to that described above for alternative A, except that the constituent points used for the analysis were a mixture of order values (from monotypic orders), family values (from polytypic orders) and average generic values (from polytypic families) for each diet (or habitat) category. Simulation B indicated that for diet, only vertebrate eaters have significantly higher relative metabolic rates than expected (P = 0.03), and there were no significant patterns for the habitat categories (Table 3).

Discussion

The allometric exponent relating metabolic rate to body weight measured using major-axis analysis ranged between 0·73 at the generic level and 0·83 at the class level. Comparison of relative metabolic rates at the *species* level with ecological variables (diet and habitat) indicated that there are significant associations between relative metabolic rates and diet and habitat, as illustrated by McNab (1986a). For example, grass, nut and vertebrate eaters tend to have higher relative metabolic rates than frugivorous, leaf and invertebrate eaters. However, these patterns could arise through taxonomic associations.

Our simulations were designed to reveal any patterns of diet or habitat associations with relative metabolic rates that were independent of taxonomy (and, by inference, phylogeny). The results of these simulation studies do not support McNab's claim 'that basal rate of metabolism in eutherians is correlated with a finite set of factors, one of the most important being food habits' (McNab, 1986a, p. 10). Instead, we found that vertebrate eaters are the only diet category to have statistically higher metabolic rates for their body size under the conditions of both simulations. Invertebrate eaters tend to have lower relative metabolic rates, but this pattern must be regarded as tentative, since it depends upon the assumptions of the analysis performed (see below). We found no statistically significant habitat associations with relative metabolic rates.

The significant association between relative metabolic rate and a vertebrate diet that was revealed by the simulation may still be a consequence of taxonomic or other associations. For example, two monotypic orders (Cetacea and Pinnipedia) were largely responsible for the significant association between high relative metabolic rates and vertebrate diets. These high rates may be the result of the marine lifestyle of these orders. McNab (1986a) has suggested that marine mammals would be expected to have relatively higher metabolic rates as a consequence of greater heat loss to the environment. Examination of the patterns of polytypic orders may resolve this issue. If high relative metabolic rates are associated with a vertebrate diet, then the highest rates in polytypic orders should be found among vertebrate eaters. However, in two of the three polytypic orders (Marsupialia, Chiroptera and Carnivora), the highest rates are not found among vertebrate eaters (see Fig. 2). These data do not, therefore, support the view that the high relative metabolic rate found in vertebrate eaters is necessarily independent of taxonomic affiliation. Bennett & Harvey (in press) have examined the relationship between relative metabolic rate, diet and habitat in birds. Their analysis showed that aquatic seabird families have higher relative metabolic rates, but they failed to find any associations between relative metabolic rates and diet.

Why should diet affect metabolic rates? McNab (1986a) suggests that higher metabolic rates are associated with diets in which a high percentage of the food is easily digested, free from chemical deterrents, or generally available throughout the year. A diet consisting primarily of vertebrates usually has these features. According to McNab (1986a), lower relative metabolic rates are expected to be associated with foods that have chemical deterrent, low digestibility, or are only available in certain seasons. Not all invertebrates are characterized by these features, and this may partially explain the weaker association between low relative metabolic rates and an invertebrate diet.

Comparison between our alternative simulations highlights the underlying assumptions of independent data points for comparative studies. The simulation under alternative A showed that invertebrate eaters have significantly lower metabolic rates than would be expected for their body size. However, this pattern was not statistically significant under the less conservative alternative analysis B. Increasing the sample size by including families and genera from some orders (Marsupialia, Edentata, Chiroptera, Carnivora and Rodentia) to provide additional data points for statistical analyses raises the mean value of relative metabolic rates for invertebrate eaters to render the results for this diet category non-significant. This occurs because the points for three of the five orders are above the mean value (see Fig. 2), and M. A. Elgar & P. H. Harvey therefore add disproportionally to the sum of the diet values. This sum becomes less negative, and thus the probability of it exceeding a random expectation is reduced. Usually, an analysis with smaller sample sizes (such as alternative A) fails to reveal significant patterns, but this was not the case in our simulations; the lower relative metabolic rate of invertebrate eaters was no longer significant when the sample size was increased.

We conclude that many of the correlations between diet and relative metabolic rates can equally well be described by taxonomic associations, and therefore we are not persuaded by McNab's contention that 'the contribution of phylogeny to basal metabolic rates seems . . . to be modest, most of its apparent influence being due to a correlation of food habits with phylogeny' (McNab, 1986a, p. 8). We are not arguing here that taxonomic association should take precedence over ecological associations, merely that other variables may be relevant. The associations between diet and habitat with basal metabolic rates are not so convincing as McNab's (1980, 1986a) claim. In this paper, we have demonstrated that phylogeny must be taken into account when seeking associations between metabolic rate, behaviour and ecology.

Acknowledgments

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Appendix: Basal metabolic rate (BMR), body weight, diet and habitat of 265 species of mammals from 18 orders. Metabolic rate is given as mass specific, although for the statistical analysis it was measured as O_2 h⁻¹.

Monotremata Tachyglossidae Tachyglossus aculeatus Tornithorhynchidae Ornithorhynchus anatinus Marsupialia Didelphidae Marmosa microtarsus Didelphis marsupialis Dasyuridae Planigale gilesi Tachyglossidae Tachyglossida	Terrestrial Aquatic Arboreal Terrestrial Terrestrial Terrestrial	Invertebrates Invertebrates Omnivorous	weight (g) 3410·0 690·0 14·5 1350·0	0·17 0·31	McNab (1986a) McNab (1986a)
Tachyglossidae Tachyglossus aculeatus Ornithorhynchidae Ornithorhynchus anatinus Marsupialia Didelphidae Marmosa microtarsus Didelphis marsupialis Dasyuridae Planigale gilesi Tachyglossidae	Aquatic Arboreal Perrestrial	Invertebrates Invertebrates	690·0 14·5	0.31	, ,
Tachyglossus aculeatus Ornithorhynchidae Ornithorhynchus anatinus Marsupialia Didelphidae Marmosa microtarsus Didelphis marsupialis Dasyuridae Planigale gilesi T	Aquatic Arboreal Perrestrial	Invertebrates Invertebrates	690·0 14·5	0.31	, ,
Ornithorhynchidae Ornithorhynchus anatinus Marsupialia Didelphidae Marmosa microtarsus Didelphis marsupialis Dasyuridae Planigale gilesi T	Aquatic Arboreal Perrestrial	Invertebrates Invertebrates	690·0 14·5	0.31	, ,
Ornithorhynchus anatinus Marsupialia Didelphidae Marmosa microtarsus Didelphis marsupialis Dasyuridae Planigale gilesi A	Arboreal Cerrestrial	Invertebrates	14.5		McNab (1986a)
Marsupialia Didelphidae Marmosa microtarsus Didelphis marsupialis Dasyuridae Planigale gilesi T	Arboreal Cerrestrial	Invertebrates	14.5		McNab (1986a)
Didelphidae Marmosa microtarsus Didelphis marsupialis Dasyuridae Planigale gilesi T	Cerrestrial Cerrestrial				
Marmosa microtarsus A Didelphis marsupialis T Dasyuridae Planigale gilesi T	Cerrestrial Cerrestrial				
Didelphis marsupialis T Dasyuridae Planigale gilesi T	Cerrestrial Cerrestrial				
Dasyuridae Planigale gilesi T	Cerrestrial	Omnivorous	1350∙0	1.79	McNab (1986a)
Planigale gilesi T			10000	0.45	McNab (1986a)
Planigale ingrami 1	errestrial	Invertebrates	9.4	1.40	McNab (1986a)
		Invertebrates	7.1	1.59	McNab (1986a)
9	Cerrestrial	Invertebrates	8.5	1.26	McNab (1986a)
	Cerrestrial	Invertebrates	43.1	0.63	Eisenberg (1981)
	Cerrestrial	Invertebrates	37·0	0.99	Tyndale-Biscoe (1973)
8 1 ,	Arboreal	Invertebrates Vertebrates	157.2	0.81	Eisenberg (1981) Eisenberg (1981)
<i>y</i>	Cerrestrial Cerrestrial	Invertebrates	88∙8 1000∙0	0·52 0·38	Tyndale-Biscoe (1973)
, 8 ,,	Terrestrial	Invertebrates	584.4	0·50 0·51	Eisenberg (1981)
3	Cerrestrial	Vertebrates	2000.0	0.31	Eisenberg (1981)
	Terrestrial	Invertebrates	1100.0	0.45	Eisenberg (1981)
	Terrestrial	Vertebrates	6700.0	0.28	Eisenberg (1981)
	Terrestrial	Invertebrates	89.0	0.87	Eisenberg (1981)
· · · · · · · · · · · · · · · · · · ·	Terrestrial	Invertebrates	14.0	1.34	Tyndale-Biscoe (1973)
*	Terrestrial	Invertebrates	24.2	0.98	Eisenberg (1981)
Thylacomyidae		111.0110014100		0 00	2100110018 (1001)
, , ,	Terrestrial	Grass	940.0	0.36	McNab (1986a)
Peramelidae					()
	Terrestrial	Invertebrates	686.0	0.47	Tyndale-Biscoe (1973)
Isoodon macrourus	Terrestrial	Invertebrates	880.0	0.45	Tyndale-Biscoe (1973)
Phalangeridae					•
-	Arboreal	Leaves	1982.0	0.32	McNab (1986a)
Burramyidae					
	Arboreal	Omnivorous	70.0	0.86	Tyndale-Biscoe (1973)
Petauridae					
Petaurus breviceps A	Arboreal	Omnivorous	128.0	0.69	Tyndale-Biscoe (1973)
Pseudocheirus peregrinus A	Arboreal	Leaves	860.0	0.33	McNab (1986a)
Macropodidae					
3	Terrestrial	Grass	2700.0	0.32	McNab (1986a)
	Terrestrial	Grass	4796.0	0.29	Tyndale-Biscoe (1973)
*	Terrestrial	Grass	32490.0	0.18	Tyndale-Biscoe (1973)
8	Arboreal	Leaves	6960.0	0.21	McNab (1986a)
Phascolarctidae	. , ,				
	Arboreal	Leaves	4765.0	0.22	McNab (1986a)
Edentata					
Myrmecophagidae	P 1	Town of allowed a	20,000.0	0.00	M-N-1 (4000)
, ,	Cerrestrial	Invertebrates	30600.0	0.09	McNab (1986a)
	Cerrestrial Cerrestrial	Invertebrates Invertebrates	3500·0 3500·0	0.26	McNab (1986a)
5	Terrestrial	Invertebrates	240.0	0·25 0·48	McNab (1986a) McNab (1986a)
· ·	ellestiiai	invertebrates	240.0	0.40	MCNab (1900a)
Bradypodidae Bradypus variagatus	Arboreal	Leaves	3790.0	0.18	McNab (1986a)
	Arboreal	Leaves	4250.0	0.19	McNab (1986a)
Dasypodidae	** DOLOGI	Douves	1230 0	0.13	11101400 (10000)
V 1	Γerrestrial	Invertebrates	8190.0	0.15	McNab (1986a)
<u>*</u>	Cerrestrial	Invertebrates	1740.0	0.23	McNab (1986a)
	Γerrestrial	Invertebrates	45 190.0	0.07	McNab (1986a)
	Γerrestrial	Invertebrates	3810.0	0.21	McNab (1986a)
	Γerrestrial	Invertebrates	1160.0	0.18	McNab (1986a)
* *	Γerrestrial	Invertebrates	3320.0	0.24	McNab (1986a)

Appendix: continued

Taxon	Habitat	Diet	Body weight (g)	BMR $(0_2 g^{-1} h^{-1})$	Source
TAXUII	Habitat	Diet	weight (g)	(U ₂ g n)	Source
Chaetophractus nationi	Terrestrial	Invertebrates	2150.0	0.26	McNab (1986a)
Chaetophractus vellerosus	Terrestrial	Invertebrates	1110.0	0.28	McNab (1986a)
Chaetophractus villosus	Terrestrial	Invertebrates	4540.0	0.18	McNab (1986a)
Insectivora					
Tenrecidae					
Tenrec ecaudatus	Aquatic	Invertebrates	790.0	0.33	McNab (1986a)
Setifer setosus	Terrestrial	Invertebrates	530.0	0.23	McNab (1986a)
Chrysochloridae	m				
Amblysomus hottentotus	Terrestrial	Invertebrates	70.0	1.21	McNab (1986a)
Erinaceidae	m 1		4500	0.00	3.6.37.1 (cono.)
Erinaceus albiventris	Terrestrial	Invertebrates	450.0	0.33	McNab (1986a)
Erinaceus europaeus	Terrestrial	Invertebrates	889.0	0.48	McNab (1986a)
Hemiechinus auritus	Terrestrial	Invertebrates	400.0	0.38	McNab (1986a)
Paraechinus aethiopus	Terrestrial	Invertebrates	450.0	0.25	McNab (1986a)
Soricidae Sorex araneus	Townsatnial	Investable	9.0	0.00	Hamalii (1004)
	Terrestrial	Invertebrates	8.9	9.08	Hanski (1984)
Sorex cinerous	Terrestrial Terrestrial	Invertebrates Invertebrates	4.9	11.67	Hanski (1984) McNab (1986a)
Sorex cinereus Sorex isodon	Terrestrial Terrestrial	Invertebrates Invertebrates	3·0 11·1	9·00 8·28	McNab (1986a) Hanski (1984)
Sorex minutissimus	Terrestrial	Invertebrates	2.5	0·20 15·48	` ,
Sorex minutus Sorex minutus	Terrestrial	Invertebrates	2.3	15.46	Hanski (1984)
Neomys anomalus	Terrestrial	Invertebrates	13.4	4.98	Hanski (1984) McNab (1986a)
Neomys anomaius Neomys fodiens	Terrestrial	Invertebrates	17.8	6.79	Hanski (1984)
Blarina brevicauda	Terrestrial	Invertebrates	21.0	2.50	McNab (1986a)
Notiosorex crawfordi	Terrestrial	Invertebrates	4.0	3.27	McNab (1986a)
Crocidura russula	Terrestrial	Invertebrates	13.7	1.9	McNab (1986a)
Talpidae	refrestrar	mverteblates	13-7	1.3	Wichab (1900a)
Scalopus aquaticus	Terrestrial	Invertebrates	48.0	1.41	McNab (1986a)
Tupaiidae	refrestria	inverteblates	10 0	1 11	Wicivab (1500a)
Tupaia glis	Arboreal	Invertebrates	180.0	0.93	McNab (1986a)
Urogale everetti	Arboreal	Invertebrates	252.0	0.86	McNab (1986a)
Chiroptera	Tirborcai	mvertebrates	202 0	0 00	Wicivab (1500a)
Pteropodidae					
Rousettus aegypticus	Arboreal	Fruit	146.0	0.84	McNab (1986a)
Pteropus poliocephalus	Arboreal	Fruit	598.0	0.53	McNab (1986a)
Pteropus scapulatus	Arboreal	Fruit	362.0	0.67	McNab (1986a)
Dobsonia minor	Arboreal	Fruit	87.0	1.26	McNab (1986a)
Cynopterus brachyotis	Arboreal	Fruit	37.0	1.27	McNab (1986a)
Eonycteris spelaea	Arboreal	Pollen	52.0	0.93	McNab (1986a)
Synconycteris australis	Arboreal	Pollen	17.5	1.93	McNab (1986a)
Rhinopomatidae					(22244)
Megaloglossus woermanni	Arboreal	Pollen	12.4	1.75	McNab (1986a)
Megadermatidae					
Macroderma gigas	Arboreal	Vertebrates	148.0	0.94	McNab (1986a)
Noctilionidae					, ,
Noctilio leporinus	Arboreal	Vertebrates	61.0	1.16	McNab (1986a)
Noctilio? labialis	Arboreal		27.0	1.17	McNab (1986a)
Phyllostomatidae					, ,
Tonatia bidens	Arboreal	Invertebrates	27.4	2.10	McNab (1986a)
Phyllostomus discolor	Arboreal	Invertebrates	33.5	1.43	McNab (1986a)
Phyllostomus hastatus	Arboreal	Invertebrates	84.2	1.19	McNab (1986a)
Chrotopterus auritus	Arboreal	Vertebrates	96.0	1.06	McNab (1986a)
Glossophaga soricina	Arboreal	Pollen	9.6	2.25	McNab (1986a)
Leptonycteris sanborni	Arboreal	Pollen	22.0	2.00	McNab (1986a)
Anoura caudifer	Arboreal	Pollen	11.5	3.05	McNab (1986a)
Carollia perspecillata	Arboreal	Fruit	14.9	2.11	McNab (1986a)
Rhinophylla pumilio	Arboreal	Fruit	9.5	1.71	McNab (1986a)
Sturnira lilium	Arboreal	Fruit	21.0	1.79	McNab (1986a)
Uroderma bilobatum	Arboreal	Fruit	16.2	1.64	McNab (1986a)
Vampyrops lineatus	Arboreal	Fruit	22.0	1.47	McNab (1986a)

Appendix: continued

			Body	BMR	
Taxon	Habitat	Diet	weight (g)	$(0_2 \text{ g}^{-1} \text{ h})$	-1) Source
Artibeus concolor	Arboreal	Fruit	19.7	1.67	McNab (1986a)
Artibeus jamaicensis	Arboreal	Fruit	45.0	1.25	McNab (1986a)
Artibeus lituratus	Arboreal	Fruit	70.0	1.21	McNab (1986a)
Desmodontidae	Miborear	rruit	70.0	1.77	Wichab (1900a)
Desmodolitidae Desmodus rotundus	Arboreal	Blood	29.0	1.18	McNab (1986a)
	Arboreal	Blood	366.0	1.02	
Diaemus youngi		Blood			McNab (1986a) McNab (1986a)
Diphylla ecaudata	Arboreal	B1000	278.0	1.39	Michab (1986a)
Molossidae	. 1 1	·	500) () (((((((((((((((((
Eumops perotis	Arboreal	Invertebrates	56.0	0.71	McNab (1986a)
Molossus molossus	Arboreal	Invertebrates	16.0	1.44	McNab (1986a)
Vespertilionidae					
Histiotus velatus	Arboreal	Invertebrates	11.2	1.40	McNab (1986a)
Primates					
Lemuridae					
Lemur fulvus	Arboreal	Leaves	2419.0	0.32	McNab (1986a)
Lorisidae					
Nycticebus coucang	Terrestrial	Invertebrates	1300.0	0.24	McNab (1986a)
Perodicticus potto	Arboreal	Fruit	1000.0	0.36	McNab (1986a)
Arctocebus calabarensis	Arboreal	Omnivorous	206.0	0.64	Hildwein (1972)
Euoticus elegantulus	Arboreal	Omnivorous	262.0	0.82	Hildwein (1972)
Callitrichidae					
Cebuella pygmaea	Arboreal	Fruit	105.0	0.94	Morrison & Middleton (1967)
Saguinus geoffroyi	Arboreal	Omnivorous	225.0	1.04	Scholander <i>et al.</i> (1950
Cebidae					
Aotus trivirgatus	Arboreal	Fruit	991.0	0.45	Goffart (1977)
Saimiri sciureus	Arboreal	Fruit	590.0	0.83	Eisenberg (1981)
Cercopithecidae					
Macaca mulatta	Arboreal	Fruit	5380.0	0.37	Bruhn (1934)
Cercocebus torquatus	Arboreal	Fruit	4100.0	0.41	Bruhn (1934)
Papio anubis	Terrestrial	Omnivorous	9500.0	0.30	Proppe & Gale (1970)
Papio papio	Terrestrial	Omnivorous	6230.0	0.41	Bruhn (1934)
Pongidae					
Pongo pygmaeus	Arboreal	Fruit	16200.0	0.30	Bruhn (1934)
Pan troglodytes	Arboreal	Omnivorous	36900.0	0.26	Bruhn (1934)
Hominidae					
Homo sapiens	Terrestrial	Omnivorous	70000.0	0.21	R.D. Martin, pers. com
arnivora					
Canidae					
Alopex lagopus	Terrestrial	Vertebrates	6000.0	0.73	Eisenberg (1981)
Vulpes vulpes	Terrestrial	Vertebrates	9000.0	0.55	Eisenberg (1981)
Lycaon pictus	Terrestrial	Vertebrates	8750.0	0.67	McNab (1986a)
Fennecus zerda	Terrestrial	Invertebrates	1106.0	0.36	McNab (1986a)
Ursidae					,
Ursus americanus	Terrestrial	Omnivorous	77270.0	0.36	Eisenberg (1981)
Procyonidae					
Potos flavus	Arboreal	Fruit	2400.0	0.32	McNab (1986a)
Mustelidae	rinborear	Truit	21000	0 02	111011415 (15554)
Mustela erminea	Terrestrial	Vertebrates	227.0	1.88	McNab (1986a)
Mustela erilinea Mustela frenata	Terrestrial	Vertebrates	297.0		, ,
,				0.95	McNab (1986a)
Mustela nivalis	Terrestrial	Vertebrates	77.0	2.29	McNab (1986a)
Mustela vison	Terrestrial	Vertebrates	660.0	0.74	McNab (1986a)
Martes americanus	Terrestrial	Vertebrates	1038.0	0.66	McNab (1986a)
Martes martes	Terrestrial	Vertebrates	920.0	0.80	McNab (1986a)
Gulo gulo	Terrestrial	Vertebrates	12700.0	0.46	McNab (1986a)
Meles meles	Terrestrial	Invertebrates	11050.0	0.27	McNab (1986a)
Lutra lutra	Aquatic	Vertebrates	10000.0	0.45	McNab (1986a)
Enhydra lutris	Aquatic	Vertebrates	18000.0	0.72	McNab (1986a)
Viverridae					
Nandinia binotata	Arboreal	Omnivorous	4270.0	0.27	McNab (1986a)

Appendix: continued

			Podu	DMD	
Taxon	Habitat	Diet	Body weight (g)	BMR $(0_2 \text{ g}^{-1} \text{ h}^{-1})$	Source
				(-28)	
Arctogalidia trivirgata	Arboreal	Omnivorous	2013.0	0.30	McNab (1986a)
Paradoxurus hermaphroditus	Arboreal	Omnivorous	3410.0	0.21	McNab (1986a)
Arctictis binturong	Arboreal	Omnivorous	14280.0	0.16	McNab (1986a)
Herpestes auropunctatus	Terrestrial	Vertebrates	611.0	0.75	McNab (1986a)
Hyaenidae					
Proteles cristata	Terrestrial	Invertebrates	7710.0	0.25	McNab (1986a)
Felidae	m	** . 1 .			774
Felis silvestris	Terrestrial	Vertebrates	3260.0	0.71	Eisenberg (1981)
Acinonyx jubatus	Terrestrial	Vertebrates	39000.0	0.35	McNab (1986a)
Pinnipedia					
Phocidae					
Phoca fasciata	Aquatic	Vertebrates	54000.0	0.39	McNab (1986a)
Phoca vitulina	Aquatic	Vertebrates	27400.0	0.48	McNab (1986a)
Pagophilus groenlandicus	Aquatic	Vertebrates	38600.0	0.38	McNab (1986a)
Cetacea					
Delphinidae					
Tursiops truncatus	Aquatic	Vertebrates	175000.0	0.34	McNab (1986a)
Phocoenidae					
Phocoena phocoena	Aquatic	Vertebrates	28500.0	0.68	McNab (1986a)
Proboscidea					
Elephantidae					
Elephas maximus	Terrestrial	Leaves	2730000.0	0.15	Eisenberg (1981)
Perissodactyla		200.00			
Equidae					
Equis caballus	Terrestrial	Grass	260 000 0	0.25	Eisenberg (1981)
	Terrestrar	Grass	200 000 0	0.23	Lisemberg (1901)
Hyracoidea					
Procaviidae		*	2010.0	0.40	M M 1 (4000)
Dendrohyrax dorsalis	Arboreal	Leaves	2210.0	0.42	McNab (1986a)
Heterohyrax brucei	Terrestrial	Leaves	1660.0	0.43	McNab (1986a)
Procavia capensis	Terrestrial	Leaves	2630.0	0.41	McNab (1986a)
Procavia habessinica	Terrestrial	Leaves	2250.0	0.41	McNab (1986a)
Procavia johnstoni	Terrestrial	Leaves	2750.0	0.45	McNab (1986a)
Tubulidentata					
Orycteropidae					
Orycteropus afer	Terrestrial	Invertebrates	48000.0	0.13	McNab (1986a)
Artiodactyla					
Suidae					
Sus scrofa	Terrestrial	Omnivorous	75 000.0	0.11	Eisenberg (1981)
Tayassuidae					
Tayassu tajacu	Terrestrial	Grass	20200.0	0.29	McNab (1986a)
Camelidae					
Camelus dromedarius	Terrestrial	Grass	$407000 \cdot 0$	0.10	McNab (1986a)
Cervidae					
Cervus elaphus	Terrestrial	Grass	58000.0	0.28	McNab (1986a)
Rangifer tarandus	Terrestrial	Grass	94000.0	0.25	McNab (1986a)
Odocoileus virginianus	Terrestrial	Grass	58590.0	0.45	McNab (1986a)
Capreolus capreolus	Terrestrial	Grass	21500.0	0.40	McNab (1986a)
Antilocapridae					
Antilocapra americanus	Terrestrial	Grass	32000.0	0.28	McNab (1986a)
Bovidae		_			
Tragelaphus oryx	Terrestrial	Grass	150000.0	0.24	McNab (1986a)
Bos taurus	Terrestrial	Grass	272000.0	0.17	Eisenberg (1981)
Kobus ellipsiprymnus	Terrestrial	Grass	100000.0	0.27	McNab (1986a)
Connochaetus taurinus	Terrestrial	Grass	140000.0	0.20	McNab (1986a)
Oreamnos americanus	Terrestrial	Grass	32000.0	0.26	McNab (1986a)
Capra sp.	Terrestrial	Grass	36 000.0	0.19	McNab (1986a)
Ovis aries	Terrestrial	Grass	30000.0	0.34	Eisenberg (1981)
Ovis canadensis	Terrestrial	Grass	65 000.0	0.34	McNab (1986a)

Appendix: continued

The state of the s	** 1 :	D	Body	BMR	0	
laxon	Habitat	Diet	weight (g)	$(0_2 g^{-1} h^{-1})$	Source	
Pholidota						
Manidae						
Manis crassicaudata	Terrestrial	Invertebrates	15910.0	0.07	McNab (1986a)	
Manis javanica	Terrestrial	Invertebrates	4220.0	0.26	McNab (1986a)	
Manis tricuspis	Terrestrial	Invertebrates	2730.0	0.33	McNab (1986a)	
Rodentia						
Sciuridae						
Sciurus aberti	Arboreal	Seeds/Nuts	624.0	0.69	McNab (1986a)	
Tamiasciurus hudsonicus	Arboreal	Seeds/Nuts	224.0	1.09	McNab (1986a)	
Spermophilus citellus	Terrestrial	Omnivorous	240.0	0.95	Hart (1971)	
Spermophilus leucums?	Terrestrial	Omnivorous	96.0	1.00	Hart (1971)	
Spermophilus tereticaudus	Terrestrial	Omnivorous	129.0	1.00	Hart (1971)	
Spermophilus undulatus	Terrestrial	Omnivorous	750.0	0.90	Hart (1971)	
Tamias alpinus	Arboreal	Seeds/Nuts	39.0	1.48	McNab (1986a)	
Tamias amoenus	Arboreal	Seeds/Nuts	57.0	1.45	McNab (1986a)	
Tamias striatus	Arboreal	Seeds/Nuts	107.0	1.25	McNab (1986a)	
Glaucomys volans	Arboreal	Seeds/Nuts	70.0	1.29	McNab (1986a)	
Geomyidae						
Geomys pinetis	Fossorial	Roots	203.0	0.67	Hart (1971)	
Heteromyidae	_	_ ,				
Perognathus californicus	Terrestrial	Seeds/Nuts	22.0	1.00	Hart (1971)	
Perognathus longimembrus	Terrestrial	Seeds/Nuts	8.2	2.00	Hart (1971)	
Microdipodops pallidus	Terrestrial	Seeds/Nuts	15.0	1.50	Hart (1971)	
Dipodomys agilis	Terrestrial	Seeds/Nuts	61.0	1.02	Hart (1971)	
Dipodomys merriami	Terrestrial	Seeds/Nuts	37.0	1.29	Hart (1971)	
Dipodomys microps	Terrestrial	Leaves	57.0	1.17	McNab (1986a)	
Dipodomys panamintinus	Terrestrial	Seeds/Nuts	57.0	1.20	Hart (1971)	
Liomys irroratus	Terrestrial	Seeds/Nuts	48.0	1.10	Hart (1971)	
Liomys salvini	Terrestrial	Seeds/Nuts	44.0	1.07	Hart (1971)	
Heteromys anomalus	Arboreal	Seeds/Nuts	69.0	1.45	McNab (1986a)	
Muridae	m 1	0 1 /21	0.0	4.04	II + (40E4)	
Reithrodontomys megalotis	Terrestrial	Seeds/Nuts	9.0	1.94	Hart (1971)	
Peromyscus californicus	Terrestrial	Seeds/Nuts	47.8	1.02	Hart (1971)	
Peromyscus crinitus	Terrestrial	Seeds/Nuts	19.0	1.55	Hart (1971)	
Peromyscus eremicus	Terrestrial	Seeds/Nuts	20.8	1.55	Hart (1971)	
Peromyscus leucopus	Terrestrial	Seeds/Nuts	26.0	2.20	Eisenberg (1981)	
Peromyscus maniculatus	Terrestrial	Seeds/Nuts Seeds/Nuts	19.0	1.90	Hart (1971) Hart (1971)	
Peromyscus megalops	Terrestrial		66.0	1.40	, ,	
Peromyscus sitkensis	Terrestrial	Seeds/Nuts	28.0	1.65	Hart (1971)	
Peromyscus thomasi	Terrestrial	Seeds/Nuts Seeds/Nuts	111.0	1·10 1·70	Hart (1971)	
Peromyscus truei Onychomys terridus	Terrestrial Terrestrial	Invertebrates	33·0 19·0	1.70	Hart (1971) McNab (1986a)	
	Terrestrial	Grass	7.3	2.00	Hart (1971)	
Baiomys taylori Oxymycterus roberti	Terrestrial	Invertebrates	84.0	1.09	McNab (1986a)	
Sigmodon hispidus	Terrestrial	Grass	141.0	1.09	McNab (1986a)	
Neotoma cinerea	Terrestrial	Leaves	321.0	0.78	McNab (1986a)	
Neotoma cinerea Neotoma fuscipes	Terrestrial	Leaves	187.0	0.78	McNab (1986a)	
Neotoma labigula	Terrestrial	Leaves	194.0	0.73	McNab (1986a)	
Neotoma lapida	Terrestrial	Leaves	120.0	0.73	Hart (1971)	
Cricetus cricetus	Terrestrial	Omnivorous	400.0	0.71	Hart (1971)	
Mesocricetus auratus	Terrestrial	Omnivorous	98.0	1.50	Hart (1971)	
Spalax leucodon	Fossorial	Roots	208.0	0.77	Hart (1971)	
Tachyoryctes splendens	Fossorial	Roots	203.0	0.77	Hart (1971)	
Dicrostonyx groenlandicus	Terrestrial	Leaves	61.0	1.55	Hart (1971)	
Dicrostonyx groenianaicus Dicrostonyx torquatus	Terrestrial	Leaves	47.0	1.97	McNab (1986a)	
Lemmus sibericus	Terrestrial	Grass	64.0	2.47	McNab (1986a)	
Clethrionomys gapperi	Terrestrial	Seeds/Nuts	16.5	3.60	Eisenberg (1981)	
Clethrionomys glareolus	Terrestrial	Seeds/Nuts	19.8	2.80	Hart (1971)	
Clethrionomys rufocanus	Terrestrial	Seeds/Nuts	27.5	2.00	Hart (1971)	
Alticola roylei	Terrestrial	Grass	53.0	2.30	McNab (1986a)	

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			Body	BMR	
Taxon	Habitat	Diet	weight (g)	$(0_2 g^{-1} h^{-1})$	Source
Arvicola richardsoni	Terrestrial	Grass	51.0	1.74	McNab (1986a)
Arvicola terrestris	Terrestrial	Grass	97.0	1.16	McNab (1986a)
Ondatra zibethicus	Terrestrial	Grass	842.0	0.82	McNab (1986a)
Neofiber alleni	Terrestrial	Grass	276.0	0.85	McNab (1986a)
Phenacomys intermedius	Terrestrial	Leaves	26.0	3.00	McNab (1986a)
Microtus arvalis	Terrestrial	Grass	20.0	2.50	Hart (1971)
Microtus californicus	Terrestrial	Grass	44.0	1.55	McNab (1986a)
Microtus longicaudus	Terrestrial	Grass	27.0	2.67	McNab (1986a)
Microtus mexicanus	Terrestrial	Grass	28.0	1.63	McNab (1986a)
Microtus montanus	Terrestrial	Grass	31.0	2.65	McNab (1986a)
Microtus nivalis	Terrestrial	Grass	35.0	3.06	McNab (1986a)
Microtus ochragaster	Terrestrial	Grass	51.0	1.18	McNab (1986a)
Microtus oeconomus	Terrestrial	Grass	32.0	2.50	McNab (1986a)
Microtus pennsylvanicus	Terrestrial	Grass	38.0	1.93	McNab (1986a)
Microtus pinetorum	Terrestrial	Grass	25.0	1.98	McNab (1986a)
Microtus agrestis	Terrestrial	Grass	22.0	2.99	McNab (1986a)
Lagurus curtatus	Terrestrial	Leaves	29.0	1.56	McNab (1986a)
Meriones unguiculatus	Terrestrial	Omnivorous	70.0	1.40	Hart (1971)
Micromys minutus	Terrestrial	Seeds/Nuts	6.0	6.70	Hart (1971)
Golunda ellioti	Terrestrial	Grass	56.0	1.08	McNab (1986a)
Lemniscomys griselda	Terrestrial	Grass	51.0	1.21	McNab (1986a)
Rattus norvegicus	Terrestrial	Omnivorous	237.0	1.32	Hart (1971)
Mus musculus	Terrestrial	Seeds/Nuts	20.5	3.40	Eisenberg (1981)
Zapodidae					. . ,
Zapus hudsonius	Terrestrial	Seeds/Nuts	25.0	1.50	Hart (1971)
Napaeozapus insignia	Terrestrial	Omnivorous	22.0	1.80	Hart (1971)
Caviidae					
Cavia porcellus	Terrestrial	Grass	570.0	0.70	Hart (1971)
Dasyproctidae					
Cuniculus paca	Arboreal	Fruit	4507.0	0.44	McNab (1986a)
Dasyprocta azarea	Arboreal	Seeds/Nuts	3849.0	0.49	McNab (1986a)
Dasyprocta leporina	Arboreal	Seeds/Nuts	2687.0	0.58	McNab (1986a)
Chinchillidae					
Chinchilla lanigera	Terrestrial	Grass	403.0	0.70	McNab (1986a)
Capromyidae					
Capromys pilorides	Arboreal	Leaves	2630.0	0.23	McNab (1986a)
Myocaster coypus	Terrestrial	Grass	4325.0	0.70	McNab (1986a)
Echimyidae					
Proechimys semispinosus	Arboreal	Fruit	498.0	0.63	McNab (1986a)
Bathyergidae					
Heliophobius kapeti?	Fossorial	Roots	89.0	0.87	Hart (1971)
Heterocephalus glaber	Fossorial	Roots	39.0	0.55	Hart (1971)
Lagomorpha					
Ochotonidae					
Ochotona princeps	Terrestrial	Grass	109.0	1.53	McNab (1986a)
Leporidae					
Lepus alleni	Terrestrial	Grass	3362.0	0.45	McNab (1986a)
Lepus americanus	Terrestrial	Grass	1581.0	0.90	McNab (1986a)
Lepus californicus	Terrestrial	Grass	1989.0	0.56	McNab (1986a)
Lepus timidus	Terrestrial	Grass	3004.0	0.36	McNab (1986a)
Sylvilagus audubonii	Terrestrial	Grass	702.0	0.63	McNab (1986a)
Macroscelidea					•
Macroscelidiidae					
Elephantulus edwardii	Terrestrial	Invertebrates	50.0	1.09	McNab (1986a)
Elephantulus rugescens	Terrestrial	Invertebrates	53.0	1.07	McNab (1986a)
Petrodromus tetradactylus	Terrestrial	Invertebrates	210.0	0.61	McNab (1986a)