### *Functional Ecology* 2004 **18**, 257–282

## FORUM The predominance of quarter-power scaling in biology

## V. M. SAVAGE,\*‡† J. F. GILLOOLY,§ W. H. WOODRUFF,\*‡ G. B. WEST,\*‡ A. P. ALLEN,§ B. J. ENQUIST¶ and J. H. BROWN\*§

\*The Santa Fe Institute, 1399 Hyde Park Road., Santa Fe, NM 87501 USA, ‡Los Alamos National Laboratory, Los Alamos, NM 87545 USA, §Department of Biology, The University of New Mexico, Albuquerque, NM 87131 USA, and ¶Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA

#### Summary

1. Recent studies have resurrected the debate over the value for the allometric scaling exponent that relates whole-organism metabolic rate to body size. Is it 3/4 or 2/3? This question has been raised before and resolved in favour of 3/4. Like previous ones, recent claims for a value of 2/3 are based almost entirely on basal metabolic rate (BMR) in mammals.

2. Here we compile and analyse a new, larger data set for mammalian BMR. We show that interspecific variation in BMR, as well as field metabolic rates of mammals, and basal or standard metabolic rates for many other organisms, including vertebrates, invertebrates, protists and plants, all scale with exponents whose confidence intervals include  $^{3}/_{4}$  and exclude  $^{2}/_{3}$ . Our analysis of maximal metabolic rate gives a slope that is greater than and confidence intervals that exclude both  $^{3}/_{4}$  and  $^{2}/_{3}$ .

3. Additionally, numerous other physiological rates that are closely tied to metabolism in a wide variety of organisms, including heart and respiratory rates in mammals, scale as  $M^{-1/4}$ .

**4.** The fact that quarter-power allometric scaling is so pervasive in biology suggests that different allometric relations have a common, mechanistic origin and provides an empirical basis for theoretical models that derive these scaling exponents.

Key-words: Body size, metabolic rates, physiological times, quarter-power scaling

Functional Ecology (2004) 18, 257-282

#### Introduction

Many fundamental characteristics of organisms scale with body size as power laws of the form:

 $Y = Y_0 M^b, \qquad \text{eqn 1}$ 

where Y is some characteristic such as metabolic rate, stride length or life span,  $Y_0$  is a normalization constant, M is body mass and b is the allometric scaling exponent. A longstanding puzzle in biology is why the exponent b is usually some simple multiple of  $^{1}/_{4}$  rather than a multiple of  $^{1}/_{3}$ , as would be expected from Euclidean scaling.

Renewed interest in allometry is due at least in part to recent theories that purport to explain the quarter-power scaling (West, Brown & Enquist 1997, 1999a; Banavar, Maritan & Rinaldo 1999; Banavar *et al.* 2002). These theories derive the scaling for metabolic rate based on the designs of resource distribution networks, such as animal and plant vascular systems. In particular, the model of West et al. assumes that these networks have three properties: (1) they branch hierarchically to supply all parts of three dimensional organisms; (2) they have terminal units, such as capillaries or petioles, that do not vary with body size; and (3) natural selection has optimized hydrodynamic flow through the network so that the work required to distribute resources has been minimized. This model predicts many other characteristics of plant and animal circulatory systems, including dimensions of vessels, total volume of fluid, rates of flow and delivery times. This model has been extended to explain the quarter-power scaling of many biological traits, including mitochondrial densities (West, Woodruff & Brown 2002), ontogenetic growth rates (West, Brown & Enquist 2001), the partitioning and allocation of production between plant organs such as roots, stems, leaves, and reproductive structures (Enquist & Niklas 2002; Niklas & Enquist 2002), times of life-history events (Gillooly et al. 2002; Savage et al. 2004), and population growth rates (Savage et al. 2004).

Ever since the seminal studies of Kleiber (1932) and Brody *et al.* (1934, 1945), some biologists have questioned

†Author to whom correspondence should be sent. E-mail: van@santafe.edu

whether the exponent for whole-organism metabolic rate really is  ${}^{3}/{}_{4}$  or whether it might be  ${}^{2}/{}_{3}$  as expected from Euclidean geometric scaling (Heusner 1982a,b, 1987, 1991; Kooijman 2000; Dodds, Rothman & Weitz 2001; White & Seymour 2003). These questions have focused on metabolic rate because it is such a fundamental characteristic for all organisms. It is the rate at which energy and materials are transformed within organisms and exchanged with the environment.

In the present study, we evaluate the evidence for the scaling exponents for basal metabolic rate (BMR) and other traits. We analyse three kinds of data. First, we compile and analyse a new comprehensive data set for the basal metabolic rate of mammals. Second, we present analyses of field and maximal metabolic rates for mammals, because these rates are more relevant to the normal function of free-living mammals than BMR, and we present reanalyses of data for mammalian heart and respiratory rates. Third, we perform meta-analyses (i.e. we calculate the mean and standard error) of scaling exponents reported in the literature for other biological rates and times, some of which can be measured more accurately than BMR. Finally, we identify problems with recent studies that have claimed that BMR of mammals scales as  $M^{2/3}$  (at least over a limited range of M) (Dodds et al. 2001; White & Seymour 2003). We conclude that the evidence supports the pervasiveness of quarter-power allometric scaling in biology and, by extension, the models of West et al. (1997, 1999a).

#### Historical perspective

The idea that power laws characterize size-related variation is old and well established in biology. Rubner (1883) originally observed that metabolic rate depended on organismal body size and proposed that the relationship followed from a surface-area rule (see also Bergman 1847). In the 1920s Julian Huxley investigated the body size dependence of ontogenetic growth and other biological attributes and coined the term 'allometric equation' for equation 1 (Huxley 1932; see also Thompson 1942). In the 1930s, Brody (1934, 1945) and Kleiber (1932) independently measured the wholeorganism metabolic rates of diverse kinds of birds and mammals and fitted the data with allometric equations. Their results were slightly different: Brody obtained a value of 0.73, whereas Kleiber concluded the exponent was exactly 3/4. Both investigators were surprised that the value was different from  $^{2}/_{3}$ , because they expected that metabolic rate in endotherms would vary with heat dissipation and therefore scale with body surface area, as hypothesized by Rubner. Explaining the observed exponents established a puzzle that has challenged biologists ever since.

© 2004 British Ecological Society, *Functional Ecology*, **18**, 257–282 Subsequent studies have given similar results. In a major monograph, Hemmingsen (1960) compiled data for endothermic birds and mammals, ectothermic vertebrates and invertebrates, and unicellular prokaryotes

and eukaryotes. The fitted data for each group had allometric exponents of  $b \approx 3/4$ . Extensive research on allometry in the 1970s and early 1980s was synthesized in four influential books by Peters (1983), McMahon & Bonner (1983), Calder (1984) and Schmidt-Nielsen (1984). These volumes reviewed the empirical evidence and found that it overwhelmingly supported quarterpower scaling for BMR and numerous other attributes of organismal form, function, physiology and life history. Peters (1983) remarks, 'one cannot but wonder why the power formula, in general, and the mass exponents of 3/4, 1/4, and -1/4, in particular, are so effective in describing biological phenomenon.' Calder (1984) claims, 'Despite shortcomings and criticisms [including the lack of a theoretical model], empirically most of the scaling does seem to fit  $M^{1/4}$  scaling ...'. Schmidt-Nielsen (1984) declares that, 'It has been widely accepted that the slope of the metabolic regression line for mammals is 0.75 or very close to it, and most definitely not 0.67 (as far as the "surface rule" would suggest)', and that '... it is overwhelmingly certain that the exponent differs from  $0.67 \dots$ .

As suggested by the last quote, empirical studies forced scientists to conclude that biological allometry does not reflect simple geometric scaling. Not only does whole-organism metabolism scale as  $M^{3/4}$ , but massspecific metabolic rate and most other biological rates scale as  $M^{-1/4}$  (e.g. heart and respiratory rates, stride frequencies) and most biological times scale as  $M^{1/4}$ (e.g. life spans, times to first reproduction, muscle twitch contraction times) (Lindstedt & Calder 1981).

So compelling was the empirical evidence for quarterpower scaling that several mechanistic theories were developed to explain it. None of these, however, were sufficiently general to account for the ubiquity of quarterpower scaling across diverse kinds of organisms and environments. McMahon proposed a theory of elastic similarity based on biomechanical adaptations to gravitational forces (McMahon 1973, 1975). While his arguments might apply to the bones of mammals or the trunks of trees, it is doubtful that they are applicable to aquatic or unicellular organisms. Blum (1977) suggested that quarter powers could be attributed to a fourth dimension, which he identified as time. He did not, however, present an explicit, testable model. Patterson (1992) developed a model based on diffusion of respiratory gases across boundary layers in aquatic organisms. Its application to terrestrial organisms has not been attempted and would be problematic. Barenblatt & Monin (1983) proposed that quarter-power scaling might reflect the fractal-like nature of biology, thereby anticipating West et al. (1997), but again, they did not provide a mechanistic, dynamical model.

However, quarter-power scaling has not been universally accepted. For a decade, beginning in the 1980s, Heusner presented analyses and arguments that the exponent for mammalian BMR was  $^{2}/_{3}$  rather than  $^{3}/_{4}$  (Heusner 1982a, 1982b). Heusner's criticisms were answered by Bartels (1982) and Feldman & McMahon

**259** *Quarter-power scaling in biology*  (1983) (see also Schmidt-Nielsen 1984, pp. 60–62). As a consequence, the debate subsided, the ubiquity of quarter powers was widely accepted, and there was relatively little research in allometry until the late 1990s when a series of theoretical papers appeared (West *et al.* 1997, 1999a, 2001, 2002; Enquist, Brown & West 1998; Banavar *et al.* 1999, 2002; West, Brown & Enquist 1999b; Enquist & Niklas 2001, 2002; Niklas & Enquist 2001, 2002; Gillooly *et al.* 2002; Savage *et al.* 2004).

West, Brown, Enquist and their collaborators developed detailed models for the geometry and hydrodynamics of hierarchically branched mammal and plant vascular systems that accurately predicted empirically determined allometric scaling relations for many structural and functional traits (West et al. 1997, 1999a). Extensions of these models predict the allometries of ontogenetic growth trajectories (West et al. 2001), population growth rates and other life-history attributes (Savage et al. 2004), variability in biomass, abundance and productivity of plant communities (Enquist et al. 1998; West et al. 1999b; Enquist & Niklas 2001, 2002; Niklas & Enquist 2001, 2002; Belgrano et al. 2002; Niklas, Midgely & Enquist 2003), and metabolic rates at cellular, organelle and molecular levels (West et al. 2002). The theory of West, Brown & Enquist and its extensions quantitatively explain and predict a large body of empirical measurements taken across broad scales for a variety of biological phenomena; this includes not only quarter-power allometric exponents but, just as importantly, details of hierarchical branching and hydrodynamic flow.

#### Analyses: basal metabolic rate of mammals

The debate as to whether BMR scales as  $M^{3/4}$  or  $M^{2/3}$  has recently been resurrected. Dodds *et al.* (2001) reanalysed Heusner's (1991) and some other existing data sets using different statistical methods and con-



**Fig. 1.** Plot of the combined mammalian data sets of Hart (1971), Heusner (1991), Lovegrove (2000, 2003) and White & Seymour (2003), which yields a total of 626 species data points. The numerous bars are the raw data. The regression line is fitted to the average of the logarithms for every 0·1 log unit interval of mass, represented by the squares. Note that the slope is very close to  $^{3}/_{4}$ , b = 0.737 (P < 0.0001, n = 52, 95% C.I. 0.711, 0.762), and the 95% C.I. exclude  $^{2}/_{3}$ .

cluded that the <sup>2</sup>/<sub>3</sub> exponent for BMR in mammals and birds cannot be statistically rejected and that over a limited range it is, in fact, favoured. White & Seymour (2003) compiled and analysed a large data set on BMR in mammals and reached similar conclusions. We argue here that there are two reasons why these studies are inadequate to address the generality of quarter- *vs* third-power allometric scaling. First, each study uses questionable, *ad hoc* methods. Second, these studies focus exclusively on the BMR of mammals and birds and ignore the large number of published empirical scaling relations for different taxonomic groups and for other traits, many of which are easier to measure accurately and are closely tied to metabolism.

## QUESTION 1: HOW DOES MAMMALIAN BMR SCALE?

Much of the interest in allometry has focused on mammalian BMR. There have been many studies, which have generated a large quantity of data, representing measurements for hundreds of species. The vast majority of these studies were designed to address specific questions about the physiology of mammals in particular environments or taxonomic groups. They were not designed to address the question of allometric scaling of BMR across all mammals. Consequently, these large compilations of data represent an opportunistic collection that may not be representative of the Class Mammalia. In addition, these data seriously violate assumptions of the parametric statistics used to fit regression lines and calculate allometric exponents (Sokal & Rohlf 1981). Two problems are especially serious. First, the vast majority of data are for small mammals (i.e. M < 1 kg) (see Fig. 1). Unless some correction is made for this imbalance, the calculated regression statistics (slope, intercept and confidence intervals) will be biased. Second, because BMR databases contain multiple values for species in certain genera or families and few or no values for other genera or families, the data are neither independent nor representative. For example, measurements for rodents are abundant and thus contribute an undue influence on the scaling of BMR.

#### Methods

We compiled data on mammalian BMR from the large data sets used in the previous studies of Hart (1971), Heusner (1991), Lovegrove (2000, 2003) and White & Seymour (2003). In compiling this data set we found several discrepancies between the data sets of Heusner (1991), Lovegrove (2000, 2003) and White & Seymour (2003), e.g. values that differed by an order of magnitude in mass and BMR for the same species taken from the same study. These discrepancies were the result of incorrect or changed scientific names in Heusner (1991), apparent transcription and conversion errors in Lovegrove (2000, 2003), and misplaced decimal **260** *V. M. Savage* et al.

points (e.g. the reported mass for Ursus ursinus) and the shifting of rows in the BMR column for the Order Chiroptera in the appendix of White & Seymour (2003). When different data sets contained significantly different values for the same species from the same study, we referred to the original source and used the values reported there. The original sources that were consulted are given in the References section and are listed by the relevant species data in Appendix 1. Moreover, there were many species whose scientific names have changed over the period spanned by these data sets, so the list was checked extensively in order to standardize the scientific names. All names were standardized according to Wilson & Reeder (1993), and consequently, some scientific names given here differ from the ones given in the original studies. We then eliminated duplicate data, i.e. values for the same species taken from the same study that appear in multiple data sets, keeping only one datum for each of these cases. Often, for the duplicate data there were slight differences between values reported in Heusner (1991), Lovegrove (2000, 2003) and White & Seymour (2003) due either to different methods of averaging or to differing procedures for rounding before and after conversions. In an attempt to further standardize the data, we took the datum from the most recent compilation when there was this sort of discrepancy.

For the corrected, non-duplicate data, there were still multiple, independent values for the same species. In previous data sets, subspecies were often listed. We did not differentiate at the subspecies level. To address multiple data for the same species we calculated an average of the logarithms for each species, resulting in values for 626 species. The complete metabolic rate data set and the species averages are listed in Appendix 1. We then divided these species data into equally spaced logarithmic mass bins of size 0.1, resulting in 52 bins; thus, a typical bin covers a mass range from M to  $M + \Delta M$ , where  $\Delta M = 0.1M$ . All values within each bin were averaged to give a single data point for each size class. These values are also available in Appendix 2. Note that the values for M and BMR in Appendix 2 are computed from the average of the logarithms and then rounded. Then, the binned data were plotted, and since the error in the measurements of mass, corresponding to the x-axis, are much less than the error in the measurements of BMR, corresponding to the y-axis, regression lines were fitted using Ordinary Least Squares (OLS) (Type I) regression. By distributing samples uniformly with respect to mass, mass effectively becomes a treatment effect, and the regression statistics should reliably characterize the relationship between the dependent (logarithm of BMR) and independent (logarithm of M) variables. The slopes and confidence intervals represent the effects of mass on BMR.

© 2004 British Ecological Society, *Functional Ecology*, **18**, 257–282

#### Results

The original data for all species together with the average values for the binned data are plotted in Fig. 1.

A regression line (not shown) fitted to all data gives a slope of 0.712 (P < 0.0001, n = 626, 95% CI 0.699, 0.724). Notice that these 95% CI exclude *both* <sup>2</sup>/<sub>3</sub> and <sup>3</sup>/<sub>4</sub>. However, this analysis is biased by the disproportionately large representation of small body sizes. For our study there are 477 species with M < 1 kg, leaving only 149 species with M > 1 kg. After accounting for this bias by binning the data as described above in order to obtain a uniform distribution, the slope is 0.737 (P < 0.0001, n = 52, 95% CI 0.711, 0.762). The 95% CI include <sup>3</sup>/<sub>4</sub> and exclude <sup>2</sup>/<sub>3</sub>.

# QUESTION 2: HOW DO OTHER MAMMALIAN PHYSIOLOGICAL RATES SCALE?

There are two concerns in using BMR as a standard for assessing the scaling of metabolic rate and related physiological processes in mammals. First, BMR is notoriously difficult to measure according to the standard criteria. Metabolic rate is measured by a variety of techniques, including direct calorimetry, oxygen consumption and carbon dioxide production, and is known to vary with body temperature, activity and other factors (e.g. see Schmidt-Nielsen 1984 and McNab 2002). Therefore, it is difficult to ensure that individuals are in comparable physiological states, especially across the eight orders of magnitude variation in body size for mammals. Second, since BMR requires the individuals to be resting and fasting, it is not an energetic steady state and is of questionable biological relevance. At least as relevant are two other measures of metabolic rate commonly taken by physiologists. Field metabolic rate is a measure of the average rate of energy expenditure by free-living individuals under natural conditions. Maximal metabolic rate, or  $V_{o_2,max}$ , is the rate of energy expenditure during maximum aerobic activity. While there are also problems with standardizing these rates, they represent important measures of whole-organism performance that can be used to evaluate allometric scaling. The model of West et al. argues that natural selection has optimized the delivery rates of resources to cells, which is relevant to all levels of activity. Indeed, one might suspect that natural selection has operated primarily on field metabolic rate, not basal. The theory predicts that the primary differences among metabolic states will be reflected in the normalization constants (intercepts), i.e.  $B_{0,\text{max}} > B_{0,\text{field}} > B_{0,\text{basal}}$ , but it does not preclude differences in the exponents, especially for maximal metabolic rate.

Allometric equations have been fitted to data for many structural and functional traits that are closely related to metabolic rate. The processes of resource supply require a high level of functional integration. In particular, characteristics of the circulatory and respiratory systems must be coordinated with metabolic rate. Indeed, the model of West *et al.* predicts the scaling exponents for 32 such characteristics (see Table 1 Basal, Field, and Maximal Metabolic Rates for Mammals



**Fig. 2.** Plots of the basal (Hart 1971; Heusner 1991; Lovegrove 2000; Lovegrove 2003; White & Seymour 2003), field (Nagy *et al.* 1999) and maximal metabolic rates (Pasquis *et al.* 1970; Hart 1971; Lechner 1978; Prothero 1979; Taylor *et al.* 1981; Taylor *et al.* 1988; Bishop 1999; Sapoval *et al.* 2002). The regression lines are fitted to the average of the logarithms for every 0·1 log unit interval of mass. This was done in order to give equal weighting to big and small mammals. For the basal metabolic rate only the averages are shown because the raw data is shown in Fig. 1. Both raw and averaged data for basal metabolic rate are shown in Fig. 1, but here only the averages (filled squares) are shown. For the field and maximal data, diamonds and stars are the average data, and bars and open squares are the raw data, respectively. While the slope for the maximal metabolic rate is slightly higher than that for the field or basal rates, all of the slopes are close to <sup>3</sup>/<sub>4</sub>. The slope for basal is b = 0.737 (P < 0.0001, n = 52, 95% CI 0.711, 0.762), for field is 0.749 (P < 0.0001, n = 35, 95% CI 0.697, 0.801), and for maximal is 0.828 (P < 0.0001, n = 21, 95% CI 0.758, 0.897).

in West *et al.* 1997), many of which can be measured more accurately than metabolic rate. In particular, heart and respiratory rates, which are predicted to scale as  $M^{-1/4}$ , have been measured in a variety of mammals. Consequently, analyses of these rates provide additional strong tests of the theory.

#### Methods

Data for field metabolic rates were taken from Nagy, Girard & Brown (1999). Data for maximal metabolic rates were compiled from multiple sources (Pasquis, Lacaise & Dejours 1970; Hart 1971; Lechner 1978; Prothero 1979; Taylor et al. 1981; Taylor, Longworth & Hoppeler 1988; Bishop 1999; Sapoval, Filoche & Weibel 2002). We processed the maximal metabolic rate compilations in the same way as the BMR compilations. That is, duplicate data were identified in the maximal metabolic rate compilations, and only one datum was kept in each case. Then, for the non-duplicate data, we computed an average for each species. For both field and maximal metabolic rates, as for BMR, we divided the data into body size bins, calculated an average for each bin, and performed an OLS regression analysis on the averaged data. Data for heart rates are from Brody (1945), and we quote a reported value for the exponent for heart rates from Stahl (1967). Respiratory rates are taken from Calder (1968). Once again, we binned, averaged and calculated OLS regression statistics.

© 2004 British Ecological Society, *Functional Ecology*, **18**, 257–282

#### Results

In Fig. 2 we present the data for basal, field and maximal metabolic rates. The slopes of the regression lines for binned data for basal, field and maximal metabolic rates are 0.737 (P < 0.01, n = 52, 95% CI 0.711, 0.762),  $0.749 \ (P < 0.0001, n = 35, 95\% \text{ CI } 0.695, 0.802)$  and  $0.828 \ (P < 0.0001, n = 21, 95\% \text{ CI } 0.758, 0.897),$ respectively. The 95% CI for the exponents of basal and field metabolic rates include 3/4, while for maximal metabolic rate they exclude 3/4. The slope of the binned data for field metabolic rates is almost exactly 3/4 and very similar to that calculated by Nagy, Girard & Brown who treated each of the 79 species as an independent data point: 0.749 vs 0.744, respectively. The slope of the binned data for maximal metabolic rates is slightly higher than that obtained for the original unbinned data (n = 28): 0.828 vs 0.811. As expected, the normalization constants (intercepts) are different for the three metabolic states: at 1 kg the maximal rates from the regression equation are five times field rates and field rates are three times basal rates. We conclude that field and basal metabolic rates scale similarly with exponents very close to  $^{3}/_{4}$ .

The exponent for maximal metabolic rates is greater than  ${}^{3}\!/_{4}$ . Perhaps this can be explained by selection of species or methodological differences in addition to small sample size. Alternatively, it may well reflect a fundamental difference in the scaling of this process, perhaps due to vascular and respiratory adjustments, not operable under either field or basal conditions, that support maximal activity of the muscles used in exercise. Clearly, maximal metabolic rate does not scale as  $M^{2/3}$ . This is especially relevant for considerations of surface area and heat dissipation because maximal metabolic rate maximizes heat production.

In Fig. 3 we plot the data for mammalian heart and respiratory rates. After binning, the slope for the heart rate is -0.251 (P < 0.0001, n = 17, 95% CI - 0.218, -0.285), based on 26 species. Although Stahl (1967) does not give his original data, he reported that mammalian heart rate scales exactly as -0.25 (95% CI - 0.23, -0.27). The slope for respiratory rate is -0.256 (P < 0.0001, n = 18, 95% CI - 0.187, -0.320), based on 22 species. All of these exponents are almost exactly -1/4 and are statistically different from -1/3.

#### QUESTION 3: HOW DO METABOLIC RATES IN OTHER ORGANISMS SCALE? HOW DO OTHER BIOLOGICAL RATES AND TIMES SCALE?

Seemingly lost in the detailed discussions and analyses of mammalian metabolic rates are the extensive data for other allometric scaling relations. Metabolic rates have been measured and scaling exponents have been calculated for many groups of organisms in addition to mammals. The theory of West *et al.* (1997) predicts, and previous empirical studies suggest, that wholeorganism metabolic rates in these other groups also

**262** *V. M. Savage* et al.



**Fig. 3.** Plot of (a) heart rates (Brody 1945) and (b) respiratory rates of mammals at rest (Calder 1968). The regression lines are fitted to the average of the logarithms for every 0·1 log unit interval of mass, but both the average (squares) and raw data (bars) are shown in the plots. Both slopes clearly include  $-\frac{1}{4}$  and exclude  $-\frac{1}{3}$ , for heart rate the slope is -0.251 (P < 0.0001, n = 17, 95% CI -0.221, -0.281) and for respiratory rate -0.256 (P < 0.0001, n = 18, 95% CI -0.194, -0.318).

scale as  $M^{3/4}$ . In addition, extensions and applications of the theory predict that mass-specific metabolic rates and most other biological rates scale as  $M^{-1/4}$ , and biological times, which are the inverse of rates, scale as  $M^{1/4}$ . Although largely overlooked in recent work, the seminal treatments of biological allometry (McMahon & Bonner 1983; Peters 1983; Calder 1984; Schmidt-Nielsen 1984) had reached similar conclusions by the 1980s. Recent studies have shown that these allometric equations also apply to both unicellular algae and higher plants-including both gymnosperms and angiosperms (Enquist et al. 1998; West et al. 1999b; Enquist & Niklas 2001; Niklas & Enquist 2001; Enquist & Niklas 2002; Niklas & Enquist 2002). For example, both whole plant rates of biomass production and whole plant chlorophyll content scale as  $M^{3/4}$  (Niklas 1994). Further, intraspecific rates of production for 45 species of tropical trees scale with exponents indistinguishable from the predicted  $M^{3/4}$  scaling of metabolism (Enquist *et al.* 1999).

#### Methods

© 2004 British Ecological Society, *Functional Ecology*, **18**, 257–282 The four books by McMahon & Bonner (1983), Peters (1983), Calder (1984) and Schmidt-Nielsen (1984) in the 1980s still contain the most comprehensive treatments of biological allometry, including compilations

of allometric equations for many different traits and taxonomic groups. We present meta-analyses of these data by compiling the allometric scaling exponents in histograms and by calculating the average and standard error for each histogram. Data for whole organism and mass-specific biological rates are from Peters (1983), and for biological times are from Lindstedt & Calder (1981). We also present the results of a recent compilation of rates of annual biomass production for numerous groups of plants and animals as compiled by Ernest *et al.* (2003).

Further, we reanalyse data on whole plant xylem flow from Enquist et al. (1998). Xylem flow is directly related to plant metabolic rate due to the stoichiometry of photosynthesis and respiration. When these data were collected (in litres of fluid transported vertically through the plant per day), xylem flux was measured in relation to stem diameter. To facilitate comparison with allometric equations for animals, we converted stem diameter, D (in cm), to above-ground plant mass, M (in g), using the empirical relationship  $M = 124D^{2.53}$ , as outlined by Enquist & Niklas (2001). This relation of diameter to mass is well supported both theoretically and empirically (West et al. 1999b; Enquist 2002). We then divided the data into biomass bins, calculated an average for each bin, and performed a Reduced Major Axis (RMA) regression on the averaged data. Since the biomass is only an estimate, there are larger errors in the mass data than for the other plots in this paper. Furthermore, the errors for the masses are now comparable to the errors in measurement for the whole plant xylem flow, resulting in comparable errors for the variables on the x and y-axes of our plot. Consequently, reduced major axis (RMA) regression was used to fit these data (Niklas 1994).

#### Results

Exponents of whole-organism biological rates are plotted in Fig. 4. These data (see also Fig. 4.1 in Peters 1983) show a distinct mean and mode at  ${}^{3}/{}_{4}$  and not at  ${}^{2}/{}_{3}$  ( $\overline{b} = 0.749 \pm 0.007$ , SE). These data are for metabolic and other biological rates, e.g. feeding and defecation rates, and include values for a wide variety of organisms, including insects, crustaceans, mollusks, nematodes, cnidarians, porifera, algae, protists and all classes of vertebrates; they include freshwater, marine and terrestrial organisms.

There is considerable variation around <sup>3</sup>/<sub>4</sub>. This is understandable because there are many uncontrolled sources of variation (e.g. sample size, range of variation in mass, experimental methods). Peters includes all studies that met minimal criteria, and we used all of his data.

Figure 4 shows a similar histogram for exponents of mass-specific metabolic rates and other related biological rates. Values clustered around  $-\frac{1}{4}$  ( $\overline{b} = -0.247 \pm 0.011$ , SE). Figure 4 also contains a histogram for exponents of biological times, from muscle contractions to

**Table 1.** Regression statistics for annual biomass production and population-level energy use. The group 'animals' includes mammals, birds, fish, zooplankton, insects and the protist *Paraphysomonas imperforata*. Data from Ernest *et al.* (2003)

Group	Spp. no.	Scaling exponent	95% CI	Normalization constant	95% CI	r <sup>2</sup>
Production						
Plants	387	0.759	0.76 - 0.75	10.15	10.18 - 10.12	0.995
Mammals	305	0.755	0.78 - 0.73	10.25	10.29-10.21	0.910
Birds	33	0.740	0.85 - 0.63	10.66	10.79-10.53	0.858
Fish	9	0.761	0.84 - 0.68	10.85	11.03-10.67	0.984
Animals	361	0.719	0.74 - 0.70	10.30	10.34 - 10.26	0.934

life spans. Values cluster closely around  $^{1}/_{4}$  ( $\overline{b} = 0.250 \pm 0.011$ , SE).

A summary of regression statistics from Ernest *et al.* (2003) for annual biomass production across multiple plant and animal taxa are listed in Table 1. The fitted exponents for plants, mammals, birds and fish are statistically indistinguishable from  $^{3}/_{4}$  and, apart from birds, have 95% CI that exclude  $^{2}/_{3}$ .

Figure 5 plots xylem flow rate as a function of plant mass. The RMA regression line fitted to the binned data gives an exponent of 0.736 (P < 0.0001, n = 31, 95% CI 0.647, 0.825). The regression fitted to the entire unbinned data set gives a similar exponent of 0.735 (P < 0.0001, n = 69, 95% CI 0.682, 0.788). The exponent for the binned data has confidence intervals that include both  $^{3}/_{4}$  and  $^{2}/_{3}$ , while that for the unbinned data includes only  $^{3}/_{4}$ .

#### Discussion

The results shown above raise the question: How is it that two recent studies reach the conclusion that mammalian BMR scales closer to  $M^{2/3}$  than to  $M^{3/4}$ ? This is especially puzzling because both of these studies and our analyses use much of the same data, including data compiled by Heusner (1991). The discrepancies in the exponent for mammalian BMR obviously depend on the methods of analysis. We now address these issues.

Two issues are particularly relevant. The first is whether the data points can be considered statistically independent, because the species differ in phylogenetic relatedness and closely related species tend to be more similar in body size, metabolic rate and most other biological attributes (Harvey & Pagel 1991). The second issue is that the available data for mammalian BMR are overly weighted towards species of small size. Binning the data according to intervals of logarithmic mass as described above is a reasonable but perhaps not ideal method for addressing both of these problems. By definition, it gives each size class equal weight. This prevents any size class from having an undue effect on the value of b. Moreover, because closely related species are almost always similar in size, it also prevents phylogenetic relatedness from having an undue influence. The effect of size on a function such as metabolic rate

© 2004 British Ecological Society, *Functional Ecology*, **18**, 257–282



**Fig. 4.** Histograms of the exponents of (a) biological rates (Peters 1983), (b) mass-specific biological rates (Peters 1983) and (c) biological times (Lindstedt & Calder 1981). At the top of each histogram, arrows are placed to identify the positions of the relevant third- and quarter-power exponents. Note that the peak of the histogram for biological rates is near 0.75, not 0.67 ( $\overline{b} = 0.749 \pm 0.007$ ). Moreover, the histogram for mass-specific rates peaks near -0.25, not -0.33 ( $\overline{b} = -0.247 \pm 0.011$ ), and the histogram for biological times peaks at 0.25, not 0.33 ( $\overline{b} = 0.250 \pm 0.011$ ). All errors quoted here are the standard error from the mean for the distribution. Therefore, in all cases, the majority of biological rates and times exhibit quarter-power, not third-power, scaling.

is best resolved by comparisons among species that differ in mass by several orders of magnitude, which means that the species compared are almost always distantly related.



**Fig. 5.** Plot of maximum reported xylem flux rates (litres of fluid transported vertically through a plant stem per day) for plants from Enquist *et al.* (1998). The RMA regression line is fitted to the average of the logarithm for every 0·1 log unit interval of plant biomass, but both the average (squares) and raw data (bars) are shown in the plot. The slope is 0·736 (P < 0.0001, n = 31, 95% CI 0·647, 0·825).

Both of these issues arise in the recent work by Dodds et al. (2001) and White & Seymour (2003). Dodds et al. (2001) ignore phylogeny, even to the point of combining passerines and non-passerines to calculate a single allometric equation for all birds. In this case, there is an a priori basis, supported by phylogenetic analyses, for subdividing the data into two groups of birds (Garland & Ives 2000). The passerines, which constitute about half of existing bird species, are a monophyletic lineage that resulted from an extensive and separate radiation during the Tertiary (Garland & Ives 2000). Additionally, since the work of Lasiewski & Dawson (1967) in the 1960s, physiologists have recognized that when analysed separately, the two groups have very similar exponents (e.g. 0.72-0.75). The normalization constant, however, is higher for passerines than non-passerines (Lasiewski & Dawson 1967). Since the majority of passerines are smaller than non-passerines, the effect of combining the two groups is to reduce the apparent value of the exponent. The higher normalization constant for passerines is probably due in part to their slightly but consistently higher body temperatures. White & Seymour (2003) addressed the issue of phylogeny by calculating average values of the logarithms of mammalian body size and BMR for each taxonomic level: species, genus, family and order, and then fitted regression equations for each level. This is questionable for several reasons, including greatly reducing the sample size (from 619 data points (590 species after subspecies are removed and all scientific names are standardized) to 17 orders) and total range of variation in mass (by about an order of magnitude). The latter practice artefactually reduces the calculated value of the OLS regression slope, and hence underestimates the exponent (Pagel & Harvey 1988; Harvey & Pagel 1991).

© 2004 British Ecological Society, *Functional Ecology*, **18**, 257–282 Dodds *et al.* (2001) recognized there was a preponderance of data for small mammals and a curvilinearity across the entire body size range shown in our Fig. 1. They addressed this issue by calculating regression equations after progressively eliminating data for all species above some threshold body size. As the size threshold was reduced, they found a systematic decrease in the exponent, with an apparent break at  $M \sim 10$  kg and  $b \sim ^{2}/_{3}$  below this threshold. For M > 10 kg the CI included  $^{3}/_{4}$ , and for M < 10 kg the CI did not include  $^{3}/_{4}$  and closely approached  $^{2}/_{3}$ . White & Seymour's (2003) compilation, while quite accurate and extensive, does not contain some of the data available for the largest mammals. Consequently, their data set and analysis are even more strongly biased by the values for small mammals.

The original paper by West et al. (1997), which derives a model for the mammalian arterial system, predicts that smaller mammals should show consistent deviations in the direction of higher metabolic rates than expected from  $M^{3/4}$  scaling. Thus, metabolic scaling relationships are predicted to show a slight curvilinearity at the smallest size range. Therefore, fitting a regression through an allometric metabolic rate data set that samples a disproportionate number of small mammals will artificially give a slightly shallower slope. Prior to Dodds et al. (2001), Bartels (1982) found that above a threshold of 260 g, BMR data was best fit with an exponent of 0.76, and that below this threshold, the exponent was less than  $^{2}/_{3}$  or  $^{3}/_{4}$ . Additionally, Calder (1984) noted that the smallest birds (hummingbirds) and mammals (shrews) have BMRs that are consistently above the predictions from allometry. Both Dodds et al. (2001) and White & Seymour (2003) ignore this prediction of the West et al. model. Ironically, the apparent deviation from 3/4 for small mass is therefore supportive of the West et al. (1997) model.

In addition to these statistical issues, White & Seymour (2003) use two biological arguments to adjust or exclude data. First, as shown in Gillooly *et al.* (2001), variation in body temperature may cause significant variation in BMR. White & Seymour (2003) find a weak but significant correlation between body temperature and size in mammals:

$$T_b = 35.8 + 0.21 \log M.$$
 eqn 2

They corrected their BMR data to a constant body temperature using a  $Q_{10}$  factor. Second, White & Seymour (2003) eliminated data for entire taxonomic groups (artiodactyls, macropodid marsupials, lagomorphs and shrews) because these data may not meet the strict criteria required for BMR. After using these two procedures, they found that the temperature-adjusted BMR for the remaining species or orders scaled approximately as  $M^{2/3}$ .

We can explicitly calculate the influence of body temperature on the scaling exponent. Substituting equation 2 into a  $Q_{10}$  factor, we derive that

$$b_{\text{measured}} = b_{\text{actual}} + 0.02,$$

where  $b_{\text{measured}}$  is the value of b that is measured when no correction has been made for temperature. Note **265** *Quarter-power scaling in biology*  that this agrees exactly with the difference between 0.69 and 0.67 shown in Fig. 2(a)–(b) in White & Seymour (2003). Since the difference between exponents of  $^{2}/_{3}$  and  $^{3}/_{4}$  is 0.08, variation in body temperature among mammals must play a minor role in determining whether the exponent is  $^{2}/_{3}$  or  $^{3}/_{4}$ . Additionally, by excluding certain taxa from their analysis, White & Seymour (2003) eliminate most of the smallest and largest mammals from their data set. This reduces the original 5.5 orders of magnitude variation in mass to 4.5 at the species level and to only 2.5 at the order level. Regardless of the problems of meeting the strict criteria for BMR, the exclusion of so much data clearly affects the ability to fit a power law that is representative of all mammals.

By comparing the analyses of Dodds et al. (2001) and White & Seymour (2003) with ours, it is obvious that values of b ranging from  $^{2}/_{3}$  to  $^{3}/_{4}$  can be obtained from data on mammalian BMR, depending on which data are included and how they are analysed. Our analyses and meta-analyses provide strong support for an exponent of <sup>3</sup>/<sub>4</sub>. Theoretical work also supports this value. Detailed mechanistic models of mammal and plant vascular systems both predict this scaling (West et al. 1997, 1999a; Banavar et al. 1999; Banavar et al. 2002). This is noteworthy because of the major differences between the mammal and plant systems: pulsatile vs smooth flow, and a few large tubes branching into multiple smaller ones vs a constant number of microcapillary tubes diverging in bundles at branch points. Conversely, there are no dynamic, mechanistic models to explain why the exponent should be  $^{2}/_{3}$  in all organisms. Historically, Euclidean <sup>2</sup>/<sub>3</sub> scaling was expected due to surface area to volume relations. A physical argument is that endothermic mammals and birds maintain a constant body temperature by varying metabolic heat production to match heat loss to the environment (see Bergmann 1847 and discussion in Schmidt-Nielsen 1972). If heat dissipation is some simple function of skin surface area, A (i.e. emissivity and conductivity are assumed not to change with size), one might expect that  $B \propto A \propto M^{2/3}$ . This argument lost most of its support, however, when research on endotherms showed that thermal balance is maintained by actively regulating heat exchange through changes in posture, fur and feather insulation, blood flow to peripheral tissues, and through evaporative cooling by sweating and panting, e.g. see McNab (2002).

The idea that biological allometries scale with quarter powers of body mass now rests on a strong theoretical and empirical foundation. Long before the recent surge of renewed interest in allometry, it was well established that the scaling exponents are much closer to quarters than to thirds. The extensive data compiled here, along with the new analyses, provide still further support. The evidence for quarter-power scaling is based not only on mammalian BMR, but also on a wide variety of biological rates and times in a multitude of organisms, from microbes to plants to mammals.

© 2004 British Ecological Society, *Functional Ecology*, **18**, 257–282 Peters (1983) summarized this when he wrote, 'The surface law has a number of disadvantages when used to explain the  $M^{2/3}$  law. ... Nevertheless, the simplicity of the surface law as an explanation proved so attractive that over a century of science was distorted by trying to fit observations to this inappropriate model (McMahon 1980).' Let us not waste another century.

#### Acknowledgements

We are very grateful to Morgan Ernest for help with taxonomy. V.M.S., J.F.G., G.B.W., A.P.A. and J.H.B. are grateful for the support of the Thaw Charitable Trust, a Packard Interdisciplinary Science Grant, and an NSF Biocomplexity Grant. V.M.S., W.H.W., G.B.W., B.J.E. and J.H.B. are grateful for the support of LANL/LDRD Grant 20030050DR. W.H.W. is grateful for the support of NIH Grant DK 36263, and B.J.E. is grateful for the support of an NSF CAREER award (NSF DEB-0133974). G.B.W. is also grateful for NSF Award PHY-0202180.

#### References

- Banavar, J.R., Maritan, A. & Rinaldo, A. (1999) Size and form in efficient transportation networks. *Nature* 399, 130–132.
- Banavar, J.R., Damuth, J., Maritan, A. & Rinaldo, A. (2002) Supply-demand balance and metabolic scaling. *Proceed*ings of the National Academy of Sciences USA 99, 10506– 10509.
- Barenblatt, G.I. & Monin, A.S. (1983) Similarity principles for the biology of pelagic animals. *Proceedings of the National Academy of Sciences USA* 80 (11), 3540–3542.
- Bartels, H. (1982) Metabolic rate of mammals equals the 0.75 power of their body weight. *Experimental Biology and Medicine* 7, 1–11.
- Baudinette, R.V., Churchill, S.K., Christian, K.A., Nelson, J.E. & Hudson, P.J. (2000) Energy, water balance and the roost microenvironment in three Australian cave-dwelling bats (Microchiroptera). *Journal of Comparative Physiology B* 170, 439–446.
- Belgrano, A., Allen, A.P., Enquist, B.J. & Gillooly, J.F. (2002) Allometric scaling of maximum population density: a common rule for marine phytoplankton and terrestrial plants. *Ecology Letters* 5, 611–613.
- Bergmann, C. (1847) Ueber die verhältnisse der wärmeökonomie der thiere zu ihrer grösse. *Göttinger Studien*, 595–708.
- Bishop, C.M. (1999) The maximum oxygen consumption and aerobic scope of birds and mammals: getting to the heart of the matter. *Proceedings of the Royal Society of London B* 266, 2275–2281.
- Blum, J.J. (1977) On the geometry of four-dimensions and the relationship between metabolism and body mass. *Journal of Theoretical Biology* **64** (3), 599–601.
- Bradley, W.G. & Yousef, M.K. (1975) Thermoregulatory responses in the plains pocket gopher, *Geomys bursarius*. *Comparative Biochemistry and Physiology* **52A**, 35–38.
- Brody, S. (1945) *Bioenergetics and Growth*. Reinhold, New York.
- Brody, S., Procter, R.C. & Ashworth U.S. (1934) Basal metabolism, endogenous nitrogen, creatinine and neutral sulphur excretions as functions of body weight. *University* of Missouri Agricultural Experimental Station Residential Bulletin 220, 1–40.

**266** *V. M. Savage* et al.

- Calder, W.A. (1968) III Respiratory and heart rates of birds at rest. Condor 70, 358–365.
- Calder, W.A. (1984) *Size, Function, and Life History*. Harvard University Press, Cambridge, MA.
- Dodds, P.S., Rothman, D.H. & Weitz, J.S. (2001) Reexamination of the <sup>43</sup>/<sub>4</sub>-law' of metabolism. *Journal of Theoretical Biology* **209**, 9–27.
- Enquist, B.J. (2002) Universal scaling in tree and vascular plant allometry: toward a general quantitative theory linking plant form and function from cells to ecosystems. *Tree Physiology* **22**, 1045–1064.
- Enquist, B.J., Brown, J.H. & West, G.B. (1998) Allometric scaling of plant energetics and population density. *Nature* 395, 163–165.
- Enquist, B.J. & Niklas, K.J. (2001) Invariant scaling relations across tree-dominated communities. *Nature* 410, 655–660.
- Enquist, B.J. & Niklas, K.J. (2002) Global allocation rules for patterns of biomass partitioning in seed plants. *Science* **295** (5559), 1517–1520.
- Enquist, B.J., West, G.B., Charnov, E.L. & Brown, J.H. (1999) Allometric scaling of production and life-history variation in vascular plants. *Nature* **401**, 907–911.
- Ernest, S.K.M., Enquist, B.J., Brown, J.H., Charnov, E.L., Gillooly, J.F., Savage, V.M., White, E.P., Smith, F.A., Hadly, E.A., Haskell, J.P., Lyons, S.K., Maurer, B.A., Niklas, K.J. & Tiffney, B. (2003) Thermodynamic and metabolic effects on the scaling of production and population energy use. *Ecology Letters* 6, 990–995.
- Feldman, H.A. & McMahon, T.A. (1983) The <sup>3</sup>/<sub>4</sub> mass exponent for energy-metabolism is not a statistical artifact. *Respiratory Physiology* **52**, 149–163.
- Garland, T. & Ives, A.R. (2000) Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *American Naturalist* 155 (3), 346–364.
- Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M. & Charnov, E.L. (2001) Effects of size and temperature on metabolic rate. *Science* 293, 2248–2251.
- Gillooly, J.F., Charnov, E.L., West, G.B., Savage, V.M. & Brown, J.H. (2002) Effects of size and temperature on developmental time. *Nature* **417**, 70–73.
- Hart, J.S. (1971) Rodents in Comparative Physiology of Thermoregulation, Vol. II Mammals (ed. G.C. Whittow), pp. 2–149. Academic Press, New York.
- Harvey, P.H. & Pagel, M.D. (1991) The Comparative Method in Evolutionary Biology. Oxford University Press, Oxford.
- Hemmingsen, A.M. (1960) Energy metabolism as related to body size and respiratory surfaces, and its evolution. *Reports of the Steno Memorial Hospital and Nordisk Insulin Laboratorium (Copenhagen)* 9, 6–110.
- Heusner, A.A. (1982a) Energy metabolism and body size. I. Is the 0.75 mass exponent of Kleiber a statistical artifact? *Respiratory Physiology* 48, 1–12.
- Heusner, A.A. (1982b) Energy metabolism and body size. II. Dimensional analysis and energy non-similarity? *Respiratory Physiology* 48, 13–25.
- Heusner, A.A. (1987) What does the power function reveal about structure and function in animals of different size? *Annual Review of Physiology* **49**, 121–133.
- Heusner, A.A. (1991) Size and power in mammals. *Journal of Experimental Biology* **160**, 25–54.
- Hinds, D.S. & MacMillen, R.E. (1985) Scaling of energy metabolism and evaporative water loss in heteromyid rodents. *Physiological Zoology* 58 (3), 282–298.
- Huxley, J.S. (1932) Problems in Relative Growth. Methuen, London.
- Kamau, J.M.Z., Johansen, K. & Maloiy, G.M.O. (1979) Metabolism of the slender mongoose (*Herpestes sanguineus*). *Physiological Zoology* **52**, 594–602.
- Kleiber, M. (1932) Body size and metabolism. *Hilgardia* 6, 315–353.

- Kooijman, S.A.L.M. (2000) Dynamic Energy and Mass Budgets in Biology Systems. Cambridge University Press, Cambridge.
- Lasiewski, R.C. & Dawson, W.R. (1967) A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69, 13–23.
- Lechner, A.J. (1978) Scaling of maximal oxygen-consumption and pulmonary dimension in small mammals. *Respiration Physiology* 34, 29–44.
- Lindstedt, S.L. & Calder, W.A. (1981) Body size, physiological time, and longevity of homeothermic animals. *Quarterly Review of Biology* 56 (1), 1–16.
- Lovegrove, B.G. (2000) The zoogeography of mammalian basal metabolic rate. *American Naturalist* **156**, 201–219.
- Lovegrove, B.G. (2003) The influence of climate on the metabolic rate of small mammals: a slow–fast metabolic continuum. *Journal of Comparative Physiology B* **173**, 87–112.
- McMahon, T.A. (1973) Size and shape in biology. *Science* **179**, 1201–1204.
- McMahon, T.A. (1975) Allometry and biomechanics: limb bones in adult ungulates. *American Naturalist* 109, 547– 563.
- McMahon, T.A. (1980) Scaling physiological time. Lectures on Mathematics in the Life Sciences 13, 131–133.
- McMahon, T.A. & Bonner, J.T. (1983) On Size and Life. Scientific American Library, New York.
- McNab, B.K. (1969) The economics of temperature regulation in neotropical bats. *Comparative Biochemistry and Physiology* 31, 227–268.
- McNab, B.K. (1992) A statistical analysis of mammalian rates of metabolism. *Functional Ecology* **6**, 672–679.
- McNab, B.K. (2002) The Physiological Ecology of Vertebrates: a View from Energetics. Cornell University Press, Ithaca.
- Nagy, K.A., Girard, I.A. & Brown, T.K. (1999) Energetics of free-ranging mammals, reptiles, and birds. *Annual Review* of Nutrition 19, 247–277.
- Niklas, K.J. (1994) *Plant Allometry*. University of Chicago Press, Chicago, IL.
- Niklas, K.J. & Enquist, B.J. (2001) Invariant scaling relationships for interspecific plant biomass production rates and body size. *Proceedings of the National Academy of Sciences* USA 98, 2922–2927.
- Niklas, K.J. & Enquist, B.J. (2002) On the vegetative biomass partitioning of seed plant leaves, stems, and roots. *American Naturalist* 159 (5), 482–497.
- Niklas, K.J., Midgely, J.J. & Enquist, B.J. (2003) A general model for mass-growth-density relations across treedominated communities. *Evolutionary Ecology Research* 5, 459–468.
- Pagel, M.D. & Harvey, P.H. (1988) The taxon-level problem in the evolution of mammalian brain size: facts and artifacts. *American Naturalist* 132 (3), 344–359.
- Pasquis, P., Lacaise, A. & Dejours, P. (1970) Maximal oxygen uptake in 4 species of mammals. *Respiration Physiology* 9, 298–309.
- Patterson, M.R. (1992) A mass transfer explanation of metabolic scaling relations in some aquatic invertebrates and algae. *Science* 255, 1421–1423.
- Peters, R.H. (1983) *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge.
- Prothero, J.W. (1979) Maximal oxygen-consumption in various animals and plants. *Comparative Biochemistry and Physiology A* 64, 463–466.
- Rogerson, A. (1968) Energy utilization by the eland and wildebeest. *Symposia of the Zoological Society of London* **21**, 153–161.
- Rubner, M. (1883) Ueber den Einfluss der Körpergrösse auf Stoff-und Kraftwechsel. Zeitschrift für Biologie 19, 535–562.
- Sapoval, B., Filoche, M. & Weibel, E.R. (2002) Smaller is better but not too small: a physical scale for the design of

© 2004 British

18, 257-282

Ecological Society,

Functional Ecology,

the mammalian pulmonary acinus. *Proceedings of the National Academy of Sciences USA* **99**, 10411–10416.

- Savage, V.M., Gillooly, J.F., Charnov, E.L., Brown, J.H. & West, G.B. (2004) Effects of body size and temperature on population growth. *American Naturalist* in press:.
- Schmidt-Nielsen, K. (1972) *How Animals Work*. Cambridge University Press, Cambridge.
- Schmidt-Nielsen, K. (1984) Scaling: Why Is Animal Size So Important? Cambridge University Press, Cambridge.
- Sokal, R.R. & Rohlf, F.J. (1981) *Biometry*. Freeman Co, New York.
- Stahl, W.R. (1967) Scaling of respiratory variables in mammals. Journal of Applied Physiology 22, 453–460.
- Taylor, C.R., Maloiy, G.M.O., Weibel, E.R., Lungman, V.A., Kamau, J.M.Z., Seeherman, H.J. & Heglund, N.C. (1981) Design of the mammalian respiratory system. 3. Scaling maximum aerobic capacity to body-mass: wild and domestic animals, *Respiratory Physiology* 44 (1), 25–37.
- Taylor, C.R., Longworth, K.E. & Hoppeler, H. (1988) Matching O<sub>2</sub> delivery to O<sub>2</sub> demand in muscle. II. Allometric variation in energy demand. *Oxygen Transfer from Atmosphere to Tissues* (eds N.C. Gonzalez & M.R. Fedde), pp. 171–181. Plenum Publishing Corporation, New York.
- Thompson, D'A.W. (1942) *Growth and Form*. Cambridge University Press, Cambridge.

#### Note added in proof

Through communications from Prof. Ewald Weibel, we learned that there is a paper in press (Weibel, E. R., Bacigalupe, L. D., Schmitt, B., Hoppeler, H., *Respiration Physiology*, in press) in which a larger data set (35 mammalian species based on 57 estimates) for

- Weiner, J. (1977) Energy metabolism of the roe deer. *Acta Theriologica* **22** (1), 3–24.
- West, G.B., Brown, J.H. & Enquist, B.J. (1997) A general model for the origin of allometric scaling laws in biology. *Science* 276, 122–126.
- West, G.B., Brown, J.H. & Enquist, B.J. (1999a) The fourth dimension of life: fractal geometry and allometric scaling of organisms. *Science* 284, 1677–1679.
- West, G.B., Brown, J.H. & Enquist, B.J. (1999b) A general model for the structure and allometry of plant vascular systems. *Nature* 400 (6745), 664–667.
- West, G.B., Brown, J.H. & Enquist, B.J. (2001) A general model for ontogenetic growth. *Nature* 413 (6856), 628–631.
- West, G.B., Woodruff, W.H. & Brown, J.H. (2002) Allometric scaling of metabolic rate from molecules and mitochondria to cells and mammals. *Proceedings of the National Academy of Sciences USA* **99**, 2473–2478.
- White, C.R. & Seymour, R.S. (2003) Mammalian basal metabolic rate is proportional to body mass<sup>2/3</sup>. *Proceedings of the National Academy of Sciences USA* **100**, 4046–4049.
- Wilson, D.E. & Reeder, D.M., eds. (1993) Mammal Species of the World. Smithsonian Institution Press, Washington.

Received 26 September 2003; revised 13 November 2003; accepted 21 November 2003

maximal metabolic rate is analysed. They report that maximal metabolic rate scales with an allometric exponent of 0.872 (P < 0.00001, n = 35, 95%CI 0.813–0.932). They investigated the relationship between maximal metabolic rates and mitochondrial and capillary densities in the locomotor muscle system.

© 2004 British Ecological Society, *Functional Ecology*, **18**, 257–282

## Appendix 1

Order	Family	Species	Mass (g)	BMR (W)	Species avg. mass (g)	Species avg. BMR (W)	References
Artiodactyla Artiodactyla	Antilocapridae Antilocapridae	Antilocapra americana Antilocapra americana	32 000 37 800	49·984 51·981	34 779.3	50.973	Lovegrove (2000) White & Seymour (2003)
Artiodactyla	Bovidae	Bos taurus	347 000	306.770	347 000.0	306.770	Heusner (1991)
Artiodactyla	Bovidae	Cephalophus monticola	4 200	10.075	4 200.0	10.075	Lovegrove (2000)
Artiodactyla	Bovidae	Connochaetes taurinus	196 500	230.073	196 500.0	230.073	White & Seymour (2003), Rogerson (1968)
Artiodactyla	Bovidae	Kobus ellipsiprymnus	100 000	148.949	100 000.0	148.949	Lovegrove (2000)
Artiodactyla	Bovidae	Madoqua kirkii	4 290	11.966	4 290.0	11.966	Lovegrove (2000)
Artiodactyla	Bovidae	Oreamnos americanus	32 000	46.414	32 000.0	46.414	Lovegrove (2000)
Artiodactyla	Bovidae	Ovis canadensis	65 000	123.28/	6/030.8	114.0/4	Lovegrove (2000) White & Source out (2002)
Artiodactyla	Bovidae	Ovis canadensis Panhiaanus agunastris	09 125	20.610	0.600.0	20.610	L evegreve (2000)
Artiodactyla	Bovidae	Taurotrague orux	133 300	180.150	141 403.7	100.200	Heusper (1991)
Artiodactyla	Bovidae	Taurotragus oryx	150,000	200.830	141 405 7	190 209	L ovegrove (2000)
Artiodactyla	Camelidae	Camelus dromedarius	407 000	224·779	407 000.0	224.779	Lovegrove (2000)
Artiodactyla	Camelidae	Lama glama	115 000	148.940	115 000.0	148.940	Heusner (1991)
Artiodactyla	Canidae	Cervus elaphus	67 000	112.430	67 000.0	112.430	Heusner (1991)
Artiodactyla	Cervidae	Alces alces	325 000	286.847	325 000.0	286.847	White & Seymour (2003)
Artiodactyla	Cervidae	Capreolus capreolus	21 500	46.347	21 500.0	46.347	Weiner (1977)
Artiodactyla	Cervidae	Odocoileus virginianus	58 588	142.863	61 862.5	123.447	White & Seymour (2003)
Artiodactyla	Cervidae	Odocoileus virginianus	65 320	106.670			Heusner (1991)
Artiodactyla	Cervidae	Rangifer tarandus	85 000	119.660	85 000.0	119.660	Heusner (1991)
Artiodactyla	Suidae	Sus scrofa	135 000	104.150	135 000.0	104.150	Heusner (1991)
Artiodactyla	Tayassuidae	Pecari tajacu	20 500	33.165	20 500.0	33.165	White & Seymour (2003)
Artiodactyla	Tragulidae	Tragulus javanicus	1 613	4.900	1 615.5	4.883	Heusner (1991)
Artiodactyla	Tragulidae	Tragulus javanicus	1 618	4.865	2 (00 0	7.665	Lovegrove (2000)
Carnivora	Canidae	Alopex lagopus	3 600	/*005	3 000.0	/.003	White & Seymour (2003)
Carnivora	Canidae	Canis latrans	10 000	25.167	10 148.9	19.425	L ovegrove (2000)
Carnivora	Canidae	Canis mesomelas	7 720	21.533	7 720.0	21.533	White & Seymour (2003)
Carnivora	Canidae	Cerdocvon thous	5 444	8:502	5 444.0	8.502	White & Seymour (2003)
Carnivora	Canidae	Lycaon pictus	8 750	33.010	8 750.0	33.010	Heusner (1991)
Carnivora	Canidae	Vulpes velox	1 769	4.948	1 769.0	4.948	White & Seymour (2003)
Carnivora	Canidae	Vulpes vulpes	4 440	13.623	4 580.3	13.731	White & Seymour (2003)
Carnivora	Canidae	Vulpes vulpes	4 725	13.841			White & Seymour (2003)
Carnivora	Canidae	Vulpes zerda	1 106	2.230	1 159.2	2.693	Heusner (1991)
Carnivora	Canidae	Vulpes zerda	1 215	3.252			White & Seymour (2003)
Carnivora	Felidae	Acinonyx jubatus	37 900	50.107	38 446.1	61.770	White & Seymour (2003)
Carnivora	Felidae	Acinonyx jubatus	39 000	76.148		10.000	Lovegrove (2000)
Carnivora	Felidae	Felis concolor	37 200	49.326	37 200.0	49.326	White & Seymour (2003)
Carnivora	Felidae	Herpailurus yaguarondi	8 400	9.690	8 400.0	9.690	White & Seymour (2003)
Carnivora	Felidae	Leopardus viadii	2 600	5.227	2 600.0	5.227	White & Seymour (2003)
Carnivora	Felidae	Leoparaus wiedu Lantailurus sarval	1 012	1.440	1 012.0	1.440	L ovegrove (2000)
Carnivora	Felidae	Leptanarus servar Lynx rufus	9 400	23.542	9 400.0	23.542	White & Seymour (2003)
Carnivora	Felidae	Panthera leo	98 000	94·580	98 000.0	94.580	White & Seymour (2003)
Carnivora	Felidae	Panthera onca	50 400	62.419	50 400.0	62.419	White & Seymour (2003)
Carnivora	Felidae	Panthera tigris	137 900	133.859	137 900.0	133.859	White & Seymour (2003)
Carnivora	Herpestidae	Galerella sanguinea	500	2.120	519.6	2.202	Kamau et al. (1979)
Carnivora	Herpestidae	Galerella sanguinea	540	2.287			White & Seymour (2003)
Carnivora	Herpestidae	Herpestes javanicus	611	2.248	611.0	2.248	White & Seymour (2003)
Carnivora	Herpestidae	Suricata suricatta	850	1.729	850.0	1.729	White & Seymour (2003)
Carnivora	Hyaenidae	Hyaena hyaena	34 300	31.954	34 300.0	31.954	White & Seymour (2003)
Carnivora	Hyaenidae	Proteles cristatus	7710	10.925	7 902.6	11.563	Lovegrove (2000)
Carnivora	Hyaenidae	Proteles cristatus Eina hanhana	8 100	12.239	2.050.0	6.911	White & Seymour (2003)
Carnivora	Mustelidae	Elra Darbara Enhudra lutris	2 950	67.278	2 930.0	0.811	L evegreve (2000)
Carnivora	Mustelidae	Enhydra lutris Enhydra lutris	40 000	144.150	20 832.8	20.4/2	Heusner (1991)
Carnivora	Mustelidae	Gulo gulo	12,700	31.765	12 700.0	31.765	White & Seymour (2003)
Carnivora	Mustelidae	Lutra lutra	10 000	25.104	10 000.0	25.104	White & Seymour (2003)
Carnivora	Mustelidae	Martes americana	900	3.319	966.5	3.579	White & Seymour (2003)
Carnivora	Mustelidae	Martes americana	1 038	3.860			Heusner (1991)
Carnivora	Mustelidae	Martes martes	920	4.000	920.0	4.000	White & Seymour (2003)
Carnivora	Mustelidae	Meles meles	11 050	16.647	11 050.0	16.647	White & Seymour (2003)
Carnivora	Mustelidae	Mustela erminea	75	0.930	125.5	1.276	Heusner (1991)
Carnivora	Mustelidae	Mustela erminea	210	1.750			Heusner (1991)
Carnivora	Mustelidae	Mustela frenata	225	1.344	225.0	1.344	White & Seymour (2003)
Carnivora	Mustelidae	Mustela vison	660	2.722	660.0	2.722	White & Seymour (2003)
Carnivora	Mustelidae	Spilogale putorius	624	1.674	624.0	1.674	White & Seymour (2003)
Carnivora	Mustelidae	Taxidea taxus	9 000	15.062	9 000.0	15.062	White & Seymour (2003)
Carnivora	Phoeidae	Phoca jasciata Phoca groonlandica	54 000	118.020	54 000·0	118.020	Heusper (1991)
Carnivora	Phoeidae	Phoca vitulina	150 000	72.200	27 400.0	73,200	Heusner (1991)
Carmvora	rnocluae	1 noca vitutina	27 400	15.290	2/ 400.0	15.790	11eusiiei (1991)

Order	Family	Species	Mass (g)	BMR (W)	Species avg. mass (g)	Species avg. BMR (W)	References
Carnivora	Procyonidae	Ailurus fulgens	5 740	4.898	5 740.0	4.898	White & Seymour (2003)
Carnivora	Procyonidae	Bassariscus sumichrasti	1 280	3.537	1 280.0	3.537	White & Seymour (2003)
Carnivora	Procyonidae	Nasua narica	3 670	6.733	3 670.0	6.733	White & Seymour (2003)
Carnivora	Procyonidae	Nasua nasua	3 850	5.649	3 924.3	5.591	Lovegrove (2000)
Carnivora	Procyonidae	Nasua nasua	4 000	5.534	2 210 0	1 20 1	White & Seymour (2003)
Carnivora	Procyonidae	Potos flavus Potos flavus	2 215	4.441	2 318.0	4.294	Lovegrove (2000) White & Source (2002)
Carnivora	Procyonidae	Potos flavus Potos flavus	2 343	4.441			Heusper (1001)
Carnivora	Procyonidae	Procvon cancrivorus	2 400	2.588	1 160.0	2.588	White & Seymour (2003)
Carnivora	Procyonidae	Procyon lotor	4 620	12.191	4 842.2	10.428	Lovegrove (2000)
Carnivora	Procyonidae	Procyon lotor	5 075	8.920			White & Seymour (2003)
Carnivora	Ursidae	Melursus ursinus	66 957	47.064	66 957.0	47.064	McNab (1992)
Carnivora	Viverridae	Arctictis binturong	14 280	12.747	14 280.0	12.747	White & Seymour (2003)
Carnivora	Viverridae	Arctogalidia trivirgata	2 010	3.085	2 010.0	3.085	White & Seymour (2003)
Carnivora	Viverridae	Fossa fossana	2 260	5.090	2 260.0	5.090	Heusner (1991)
Carnivora	Viverridae	Genetta tigrina	1 698	4.167	1 699.0	4.189	White & Seymour (2003)
Carnivora	Viverridae	Genetta tigrina	1 700	4.210			Heusner (1991)
Carnivora	Viverridae	Nandinia binotata	4 270	4.814	4 270.0	5.565	White & Seymour (2003)
Carnivora	Viverridae	Nandinia binotata	4 270	6.432	2 292 (	5 524	Lovegrove (2000)
Carnivora	Viverridae	Paradoxurus hormaphroditus	3 100	2.005	3 282.0	5.534	L ovogrovo (2000)
Chiroptera	Emballonuridae	Peroptery macrotis	5 410	0.065	5.0	0.065	White & Seymour (2003)
Chiroptera	Emballonuridae	Saccontervy hilineata	7.8	0.081	7.8	0.081	Lovegrove (2000)
Chiroptera	Hipposideridae	Rhinonycteris aurantius	8.27	0.090	8.3	0.090	Baudinette et al. (2000)
Chiroptera	Megadermatidae	Macroderma gigas	107.2	0.526	126.0	0.639	Baudinette et al. (2000)
Chiroptera	Megadermatidae	Macroderma gigas	148	0.776			McNab (1969)
Chiroptera	Molossidae	Eumops perotis	56	0.222	56.0	0.222	White & Seymour (2003)
Chiroptera	Molossidae	Molossus molossus	15.6	0.126	15.6	0.126	White & Seymour (2003)
Chiroptera	Molossidae	Nyctinomops laticaudatus	14	0.062	14.0	0.062	Lovegrove (2000)
Chiroptera	Molossidae	Tadarida brasiliensis	10.4	0.120	13.3	0.117	Heusner (1991)
Chiroptera	Molossidae	Tadarida brasiliensis	16.9	0.113	0.6	0.045	White & Seymour (2003)
Chiroptera	Mormoopidae	Mormoops blainvillii	8.6	0.045	8.6	0.045	White & Seymour (2003)
Chiroptera	Mormoopidae	Mormoops megalophylla Btoronotus danni	16.5	0.085	16.5	0.136	White & Seymour (2003)
Chiroptera	Mormoopidae	Pteronotus parnallii	9·4 10.2	0.083	9·4 10.2	0.171	Lovegrove (2000)
Chiroptera	Mormoopidae	Pteronotus personatus	19.2	0.128	19.2	0.128	Lovegrove (2000)
Chiroptera	Mormoopidae	Pteronotus quadridens	4.9	0.034	4.9	0.034	White & Seymour (2003)
Chiroptera	Natalidae	Natalus tumidirostris	5.4	0.046	5.4	0.046	White & Seymour (2003)
Chiroptera	Noctilionidae	Noctilio albiventris	27	0.176	27.0	0.176	McNab (1969)
Chiroptera	Noctilionidae	Noctilio leporinus	61	0.400	61.0	0.400	McNab (1969)
Chiroptera	Phyllostomidae	Anoura caudifera	11.5	0.238	11.5	0.238	McNab (1969)
Chiroptera	Phyllostomidae	Artibeus concolor	19.7	0.222	19.7	0.222	McNab (1969)
Chiroptera	Phyllostomidae	Artibeus fimbriatus	63.9	0.435	63.9	0.435	White & Seymour (2003)
Chiroptera	Phyllostomidae	Artibeus jamaicensis	45.2	0.428	46.1	0.359	McNab (1969)
Chiroptera	Phyllostomidae	Artibeus jamaicensis	4/	0.300	70.1	0.002	Heusner $(1991)$
Chiroptera	Phyllostomidae	Artibeus illuratus Cavollia parspioillata	/0.1	0.002	/0.1	0.002	McNab (1969) McNab (1960)
Chiroptera	Phyllostomidae	Chiroderma doriae	14.9	0.173	14.9	0.173	White & Seymour (2003)
Chiroptera	Phyllostomidae	Chrotopterus auritus	96.1	0.788	96.1	0.788	McNab (1969)
Chiroptera	Phyllostomidae	Desmodus rotundus	29.4	0.194	29.4	0.194	McNab (1969)
Chiroptera	Phyllostomidae	Diaemus youngi	36.6	0.208	36.6	0.208	McNab (1969)
Chiroptera	Phyllostomidae	Diphylla ecaudata	27.8	0.215	27.8	0.215	McNab (1969)
Chiroptera	Phyllostomidae	Erophylla sezekorni	16.1	0.099	16.1	0.099	White & Seymour (2003)
Chiroptera	Phyllostomidae	Glossophaga soricina	9.6	0.164	9.6	0.164	McNab (1969)
Chiroptera	Phyllostomidae	Leptonycteris curasoae	22	0.245	22.0	0.245	White & Seymour (2003)
Chiroptera	Phyllostomidae	Macrotus californicus	11.7	0.082	11.7	0.082	Lovegrove (2000)
Chiroptera	Phyllostomidae	Monophyllus redmani	8.7	0.062	8.7	0.062	White & Seymour (2003)
Chiroptera	Phyllostomidae	Phyllostomus discolor	33.5	0.267	33.5	0.267	McNab (1969)
Chiroptera	Phyllostomidae	Phyllostomus hastatus	33°0 84.2	0.216	33°0 84.2	0.216	MaNab (1960)
Chiroptera	Phyllostomidae	Platyrrhinus lineatus	21.9	0.250	21.9	0.250	McNab (1969)
Chiroptera	Phyllostomidae	Rhinophylla fischerae	9.5	0.091	9.5	0.091	Lovegrove (2000)
Chiroptera	Phyllostomidae	Rhinophylla pumilio	9.5	0.104	9.5	0.104	McNab (1969)
Chiroptera	Phyllostomidae	Sturnira lilium	21	0.190	21.4	0.237	Heusner (1991)
Chiroptera	Phyllostomidae	Sturnira lilium	21.9	0.297			McNab (1969)
Chiroptera	Phyllostomidae	Sturnira tildae	20.5	0.223	20.5	0.223	White & Seymour (2003)
Chiroptera	Phyllostomidae	Tonatia bidens	27.4	0.307	27.4	0.307	McNab (1969)
Chiroptera	Phyllostomidae	Uroderma bilobatum	16.2	0.176	16.2	0.176	McNab (1969)
Chiroptera	Phyllostomidae	Vampyressa pusilla	8.8	0.104	8.8	0.104	White & Seymour (2003)
Chiroptera	Pteropodidae	Cynopterus brachyotis	37	0.260	37.2	0.262	Heusner (1991)
Chiroptera	Pteropodidae	Cynopterus brachyotis	37.4	0.265	00.1	0.504	white & Seymour (2003)
Chiroptera	Pteropodidae	Dobsonia minor Dobsonia minor	/3./	0.415	80.1	0.204	white & Seymour (2003)
Chiloptera	reropouldae	Dousonia minor	0/	0.017			Lovegrove (2000)

Order	Family	Species	Mass (g)	BMR (W)	Species avg. mass (g)	Species avg. BMR (W)	References
Chiroptera	Pteropodidae	Dobsonia moluccensis	241.4	0.971	312.4	1.411	White & Seymour (2003)
Chiroptera	Pteropodidae	Dobsonia moluccensis	404.3	2.052			White & Seymour (2003)
Chiroptera	Pteropodidae	Dobsonia praedatrix	179.5	0.795	179.5	0.795	White & Seymour (2003)
Chiroptera	Pteropodidae	Eonycteris spelaea	51.6	0.268	51.6	0.268	Lovegrove (2000)
Chiroptera	Pteropodidae	Macroglossus minimus Magaloglossus woarmanni	15.9	0.103	15.9	0.103	L ovegrove (2000)
Chiroptera	Pteropodidae	Megalogiossus woermanni Melonycteris melanons	53.3	0.242	53.3	0.242	White & Seymour (2003)
Chiroptera	Pteropodidae	Nyctimene albiventer	28.2	0.212	29.5	0.185	Lovegrove (2000)
Chiroptera	Pteropodidae	Nyctimene albiventer	30.9	0.152			White & Seymour (2003)
Chiroptera	Pteropodidae	Nyctimene cyclotis	40.4	0.360	40.4	0.360	White & Seymour (2003)
Chiroptera	Pteropodidae	Nyctimene major	13.6	0.114	13.6	0.114	White & Seymour (2003)
Chiroptera	Pteropodidae	Paranyctimene raptor	21.3	0.170	22.4	0.152	Heusner (1991)
Chiroptera	Pteropodidae	Paranyctimene raptor	23.6	0.137	5(2.2	1.600	White & Seymour (2003)
Chiroptera	Pteropodidae	Pteropus giganteus	562·2	1.622	562·2	1.622	White & Seymour (2003)
Chiroptera	Pteropodidae	Pteropus nypometanus Pteropus poliocaphalus	520.8	1.018	520.8	1.768	White & Seymour (2003)
Chiroptera	Pteropodidae	Pteropus pumilus	194.2	0.705	194.2	0.705	White & Seymour (2003)
Chiroptera	Pteropodidae	Pteropus rodricensis	254.5	0.753	254.5	0.753	White & Seymour (2003)
Chiroptera	Pteropodidae	Pteropus scapulatus	362	1.353	362.0	1.353	White & Seymour (2003)
Chiroptera	Pteropodidae	Pteropus vampyrus	1024.3	4.486	1024.3	4.486	White & Seymour (2003)
Chiroptera	Pteropodidae	Rousettus aegyptiacus	146	0.684	146.0	0.684	White & Seymour (2003)
Chiroptera	Pteropodidae	Rousettus amplexicaudatus	91.5	0.582	91.5	0.582	White & Seymour (2003)
Chiroptera	Pteropodidae	Syconycteris australis	15.9	0.122	16.7	0.152	White & Seymour (2003)
Chiroptera	Pteropodidae	Syconycteris australis	17.5	0.188			McNab (1969)
Chiroptera	Rhinolophidae	Hipposideros galeritus	8.5	0.050	8.5	0.020	Heusner (1991)
Chiroptera	Vespertilionidae	Antrozous pallidus	22	0.104	22.0	0.104	Lovegrove (2000)
Chiroptera	Vespertilionidae	Chalinolobus gouldii	1/.5	0.141	17.5	0.112	White & Seymour (2003)
Chiroptera	Vespertilionidae	Epiesicus fuscus	10.4	0.110	13.3	0.113	Houspor (1001)
Chiroptera	Vespertilionidae	Histiotus velatus	11.2	0.088	11.2	0.088	White & Seymour (2003)
Chiroptera	Vespertilionidae	Miniopterus schreibersi	10.91	0.145	10.9	0.145	Baudinette <i>et al.</i> (2000)
Chiroptera	Vespertilionidae	Mvotis lucifugus	5.2	0.020	5.8	0.051	White & Seymour (2003)
Chiroptera	Vespertilionidae	Myotis lucifugus	6.5	0.052			Lovegrove (2000)
Chiroptera	Vespertilionidae	Myotis nigricans	3.7	0.027	3.7	0.027	Lovegrove (2000)
Chiroptera	Vespertilionidae	Myotis velifer	11.89	0.040	11.9	0.040	Heusner (1991)
Chiroptera	Vespertilionidae	Myotis vivesi	25	0.199	25.0	0.199	Lovegrove (2000)
Chiroptera	Vespertilionidae	Myotis yumanensis	5	0.047	5.0	0.047	Lovegrove (2000)
Chiroptera	Vespertilionidae	Nyctophilus geoffroyi	8	0.062	8.0	0.062	White & Seymour (2003)
Chiroptera	Vespertilionidae	Plecotus auritus	10.25	0.082	10.2	0.082	White & Seymour (2003)
Dasyuromorpha	Caluromyidae	Caluromys derbianus	329	1.1255	342.7	1.194	L ovogrovo (2000)
Dasyuromorpha	Dasvuridae	Antechinus flavines	46.5	0.252	46.5	0.252	White & Seymour (2003)
Dasyuromorpha	Dasyuridae	Antechinus stuartii	22.1	0.190	25.0	0.189	Heusner (1991)
Dasyuromorpha	Dasyuridae	Antechinus stuartii	28.2	0.189			White & Seymour (2003)
Dasyuromorpha	Dasyuridae	Antechinus swainsonii	66.9	0.351	66.9	0.351	White & Seymour (2003)
Dasyuromorpha	Dasyuridae	Dasycercus byrnei	89	0.440	100.0	0.439	Heusner (1991)
Dasyuromorpha	Dasyuridae	Dasycercus byrnei	91.7	0.400			White & Seymour (2003)
Dasyuromorpha	Dasyuridae	Dasycercus byrnei	103.5	0.456			Lovegrove (2000)
Dasyuromorpha	Dasyuridae	Dasycercus byrnei	118.2	0.462			Lovegrove (2003)
Dasyuromorpha	Dasyuridae	Dasycercus cristicauda	86	0.240	91.0	0.260	Lovegrove (2003)
Dasyuromorpha	Dasyuridae	Dasycercus cristicauda	88.8	0.260			Heusner (1991)
Dasyuromorpha	Dasyuridae	Dasycercus cristicauda	101	0.238			White & Saymour (2002)
Dasyuromorpha	Dasyuridae	Dasyurus geoffroii	1 300	2.820	1 326.7	2.991	Heusper (1991)
Dasyuromorpha	Dasyuridae	Dasyurus geoffroii	1 354	3.172	1 520 7	2 ))1	Lovegrove (2000)
Dasyuromorpha	Dasyuridae	Dasvurus hallucatus	558	1.356	571.0	1.501	White & Seymour (2003)
Dasyuromorpha	Dasyuridae	Dasyurus hallucatus	584.4	1.663			Lovegrove (2003)
Dasyuromorpha	Dasyuridae	Dasyurus maculatus	1 782	3.010	1 782.0	3.142	Heusner (1991)
Dasyuromorpha	Dasyuridae	Dasyurus maculatus	1 782	3.281			White & Seymour (2003)
Dasyuromorpha	Dasyuridae	Dasyurus viverrinus	909.9	2.310	945.3	2.260	Heusner (1991)
Dasyuromorpha	Dasyuridae	Dasyurus viverrinus	982	2.210			White & Seymour (2003)
Dasyuromorpha	Dasyuridae	Ningaui yvonnae	11.6	0.088	11.6	0.088	White & Seymour (2003)
Dasyuromorpha	Dasyuridae	Phascogale tapoatafa	14/	0.664	153.7	0.694	Lovegrove (2000)
Dasyuromorpha	Dasyuridae	1 nascogale tapoatafa Phascogale tapoatafa	157.2	0.710			I ovegrove (2003)
Dasyuromorpha	Dasyuridae	1 nuscogue iupoataja Planigale gilesi	1 <i>3</i> /-2 8.0	0.071	Q. 1	0.058	Lovegrove (2003)
Dasyuromorpha	Dasyuridae	Planigale gilesi	9.1	0.039	<i>y</i> 1	0.000	White & Sevmour (2003)
Dasyuromorpha	Dasyuridae	Planigale gilesi	9.4	0.020			Heusner (1991)
Dasyuromorpha	Dasyuridae	Planigale ingrami	7.1	0.063	8.8	0.065	White & Seymour (2003)
Dasyuromorpha	Dasyuridae	Planigale ingrami	10.8	0.067			White & Seymour (2003)
Dasyuromorpha	Dasyuridae	Planigale maculata	8.5	0.060	10.6	0.067	Heusner (1991)
Dasyuromorpha	Dasyuridae	Planigale maculata	13.1	0.074			Lovegrove (2000)
Dasyuromorpha	Dasyuridae	Planigale tenuirostris	7.1	0.063	7.1	0.063	White & Seymour (2003)

Order	Family	Species	Mass (g)	BMR (W)	Species avg. mass (g)	Species avg. BMR (W)	References
Dasyuromorpha	Dasyuridae	Pseudantechinus macdonnellensis	43.1	0.152	43.1	0.152	White & Seymour (2003)
Dasyuromorpha	Dasyuridae	Sarcophilus laniarius	5 775	7.394	6 126.8	8.664	White & Seymour (2003)
Dasyuromorpha	Dasyuridae	Sarcophilus laniarius	6 500	10.153			Lovegrove (2000)
Dasyuromorpha	Dasyuridae	Sminthopsis crassicaudata	14.1	0.110	16.0	0.121	Heusner (1991)
Dasyuromorpha	Dasyuridae	Sminthopsis crassicaudata	15.9	0.114			Lovegrove (2000)
Dasyuromorpha	Dasyuridae	Sminthopsis crassicaudata	16.4	0.122			White & Seymour (2003)
Dasyuromorpha	Dasyuridae	Smininopsis crassicaudata Sminthopsis laniger	24.2	0.123	25.8	0.141	White & Seymour (2003)
Dasyuromorpha	Dasyuridae	Sminthopsis laniger	25.8	0.141	25 0	0 141	White & Seymour (2003)
Dasyuromorpha	Dasyuridae	Sminthopsis laniger	27.4	0.150			Lovegrove (2003)
Dasyuromorpha	Dasyuridae	Sminthopsis macroura	19.35	0.126	20.6	0.128	White & Seymour (2003)
Dasyuromorpha	Dasyuridae	Sminthopsis macroura	22	0.131			Lovegrove (2000)
Dasyuromorpha	Dasyuridae	Sminthopsis murina	12.9	0.114	15.7	0.117	Lovegrove (2000)
Dasyuromorpha	Dasyuridae	Sminthopsis murina	19	0.120			White & Seymour (2003)
Dasyuromorpha	Didelphidae	Chironectes minimus	935	2.549	940.5	2.793	White & Seymour (2003)
Dasyuromorpha	Didelphidae	Chironectes minimus	946	3.061			Lovegrove (2000)
Dasyuromorpha	Didelphidae	Didelphis marsupialis	1 165	3.185	1 244.3	3.310	White & Seymour (2003)
Dasyuromorpha	Didelphidae	Didelphis marsupialis	1 329	3.440	2.946.6	5 200	Heusner (1991)
Dasyuromorpha	Didelphidae	Didelphis virginiana Didelphis virginiana	2 488	4.041	2 846.6	5.299	White & Seymour (2003)
Dasyuromorpha	Didelphidae	Lutraolina crassicaudata	5 237 812	2.265	812.0	2.265	White & Seymour (2003)
Dasyuromorpha	Didelphidae	Philander opossum	751	1.886	751.0	1.886	White & Seymour (2003)
Dasyuromorpha	Marmosidae	Gracilinanus microtarsus	13	0.106	13.0	0.106	White & Seymour (2003)
Dasyuromorpha	Marmosidae	Marmosa robinsoni	122	0.547	122.0	0.547	White & Seymour (2003)
Dasyuromorpha	Marmosidae	Metachirus nudicaudatus	336	1.144	336.0	1.144	White & Seymour (2003)
Dasyuromorpha	Marmosidae	Monodelphis brevicaudata	75.5	0.318	91.5	0.366	White & Seymour (2003)
Dasyuromorpha	Marmosidae	Monodelphis brevicaudata	111	0.421			Lovegrove (2000)
Dasyuromorpha	Marmosidae	Monodelphis domestica	104	0.335	104.0	0.335	White & Seymour (2003)
Dasyuromorpha	Myrmecobiidae	Myrmecobius fasciatus	400	0.794	438.2	0.907	White & Seymour (2003)
Dasyuromorpha	Myrmecobiidae	Myrmecobius fasciatus	480	1.036			Lovegrove (2003)
Diprotodontia	Acrobatidae	Acrobates pygmaeus	14	0.084	14.0	0.084	White & Seymour (2003)
Diprotodontia	Burramyidae	Burramys parvus	44.3	0.205	44.3	0.205	White & Seymour (2003)
Diprotodontia	Burramyidae	Cercartetus lepidus	12.6	0.105	12.6	0.105	White & Seymour (2003)
Diprotodontia	Burramyidae	Cercartetus nanus	60 70	0.288	04.9	0.311	White & Sournour (2002)
Diprotodontia	Macropodidae	Dendrolagus matschiei	6 960	7.960	6.960-0	7.960	White & Seymour (2003)
Diprotodontia	Macropodidae	Lagorchestes conspicillatus	2,660	4.749	2.660.0	4.749	White & Seymour (2003)
Diprotodontia	Macropodidae	Macropus eugenii	4 796	7.780	4 796.0	7.780	Heusner (1991)
Diprotodontia	Macropodidae	Macropus robustus	29 300	31.710	29 647.9	33.056	White & Seymour (2003)
Diprotodontia	Macropodidae	Macropus robustus	30 000	34.460			Heusner (1991)
Diprotodontia	Macropodidae	Macropus rufus	25 000	30.130	28 500.0	31.353	Heusner (1991)
Diprotodontia	Macropodidae	Macropus rufus	32 490	32.625			White & Seymour (2003)
Diprotodontia	Macropodidae	Setonix brachyurus	2 510	4.520	2 702.3	4.695	Heusner (1991)
Diprotodontia	Macropodidae	Setonix brachyurus	2 674	4.654			White & Seymour (2003)
Diprotodontia	Macropodidae	Setonix brachyurus	2 940	4.920	1// 0	0.574	Lovegrove (2000)
Diprotodontia	Petauridae	Gymnobelideus leadbeateri Bataumus huomisana	100	0.5/4	100.0	0.5/4	White & Seymour (2003)
Diprotodontia	Petauridae	Petaurus breviceps	127	0.502	129.3	0.317	Heusper (1991)
Diprotodontia	Petauridae	Petaurus brevicens	120 1	0.522			Lovegrove (2000)
Diprotodontia	Petauridae	Petaurus breviceps	132.2	0.546			Lovegrove (2003)
Diprotodontia	Phalangeridae	Spilocuscus maculatus	4 250	6.164	4 250.0	6.270	Lovegrove (2000)
Diprotodontia	Phalangeridae	Spilocuscus maculatus	4 250	6.378			White & Seymour (2003)
Diprotodontia	Phalangeridae	Trichosurus vulpecula	1 982	3.538	1 993.5	3.800	Lovegrove (2000)
Diprotodontia	Phalangeridae	Trichosurus vulpecula	2 005	4.081			White & Seymour (2003)
Diprotodontia	Phascolarctidae	Phascolarctos cinereus	4 700	5.720	4 732.4	5.744	Heusner (1991)
Diprotodontia	Phascolarctidae	Phascolarctos cinereus	4 765	5.768			White & Seymour (2003)
Diprotodontia	Potoroidae	Aepyprymnus rufescens	2 820	5.978	2 820.0	5.978	White & Seymour (2003)
Diprotodontia	Potoroidae	Bettongia gaimardi	1 385	3.5/8	1 385.0	3.5/8	White & Seymour (2003)
Diprotodontia	Potoroidae	Bettongia peniciliata	1 018	2.222	1 018.0	3.132	White & Seymour (2003)
Diprotodontia	Potoroidae	Potorous tridactylus	1 1 20	2.323	1 045.5	2.330	L ovegrove (2000)
Diprotodontia	Pseudocheiridae	Cercartetus concinnus	1 120	0.125	18.6	0.125	Lovegrove (2000)
Diprotodontia	Pseudocheiridae	Petauroides volans	1 140	3.180	1 140.5	3.191	Lovegrove (2000)
Diprotodontia	Pseudocheiridae	Petauroides volans	1 141	3.202			White & Seymour (2003)
Diprotodontia	Pseudocheiridae	Pseudocheirus peregrinus	828	2.210	859.3	2.270	Heusner (1991)
Diprotodontia	Pseudocheiridae	Pseudocheirus peregrinus	835	2.194			Lovegrove (2003)
Diprotodontia	Pseudocheiridae	Pseudocheirus peregrinus	861	2.282			White & Seymour (2003)
Diprotodontia	Pseudocheiridae	Pseudocheirus peregrinus	916	2.402			White & Seymour (2003)
Diprotodontia	Tarsipedidae	Tarsipes rostratus	10	0.162	10.0	0.162	White & Seymour (2003)
Diprotodontia	Vombatidae	Lasiorhinus latifrons	25 000	15.341	27 348.2	16.001	Lovegrove (2000)
Diprotodontia	vombatidae	Lastorninus latifrons	29 917	16.690	2 210 0	4.100	White & Seymour (2003)
Hyracoidea	Procaviidae	Heterohyrax brucei	1 287	3.733	1 604.4	3.872	Lovegrove (2000)

Order	Family	Species	Mass (g)	BMR (W)	Species avg. mass (g)	Species avg. BMR (W)	References
Hyracoidea	Procaviidae	Heterohvrax brucei	2 000	4.017			White & Seymour (2003)
Hyracoidea	Procaviidae	Procavia capensis	2 250	5.021	2 458.0	4.954	White & Seymour (2003)
Hyracoidea	Procaviidae	Procavia capensis	2 400	3.682			White & Seymour (2003)
Hyracoidea	Procaviidae	Procavia capensis	2 750	6.577			White & Seymour (2003)
Insectivora	Chrysochloridae	Amblysomus hottentotus	70	0.473	70.0	0.473	White & Seymour (2003)
Insectivora	Chrysochloridae	Chrysochloris asiatica	33	0.220	36.7	0.243	Heusner (1991)
Insectivora	Chrysochloridae	Chrysochloris asiatica	34	0.228			Lovegrove (2000)
Insectivora	Chrysochloridae	Chrysochloris asiatica	44	0.287			White & Seymour (2003)
Insectivora	Chrysochloridae	Eremitalpa granti	20	0.056	22.8	0.069	White & Seymour (2003)
Insectivora	Chrysochloridae	Eremitalpa granti	26.1	0.086			Lovegrove (2000)
Insectivora	Erinaceidae	Atelerix albiventris	450	0.828	450.0	0.828	White & Seymour (2003)
Insectivora	Erinaceidae	Echinosorex gymnura	721.2	2.816	721.2	2.816	White & Seymour (2003)
Insectivora	Erinaceidae	Erinaceus concolor	822-7	1.937	822-7	1.937	White & Seymour (2003)
Insectivora	Erinaceidae	Erinaceus europaeus	/50	1.883	1 213.5	2.434	White & Seymour (2003)
Insectivora	Erinaceidae	Erinaceus europaeus	1 191-2	2.632			Lovegrove (2000)
Insectivora	Erinaceidae	Erinaceus europaeus	2 000	2.910	451 5	0.(20	Heusner (1991)
Insectivora	Erinaceidae	Hemiechinus dethiopicus	450	0.628	451.5	0.030	L avagrava (2000)
Insectivora	Erinaceidae	Hemiechinus deiniopicus	455	0.842	208.5	0.945	Lovegrove (2000)
Insectivora	Erinaceidae	Hemiechinus auritus	397	0.842	398.3	0.843	White & Source (2000)
Insectivora	Erinaceidae	Hylomys suillus	57.8	0.335	57.8	0.225	White & Seymour (2003)
Insectivora	Sorioidao	Plavina broviaguda	20.4	0.335	20.0	0.333	L ovogrova (2000)
Insectivora	Soricidae	Blaring brovicauda	204	0.366	20 9	0 544	White & Seymour (2003)
Insectivora	Soricidae	Blarina brevicauda	20.3	0.200			Heusper (1991)
Insectivora	Soricidae	Blaring brovicauda	207	0.307			Lovegrove $(2003)$
Insectivora	Soricidae	Blarina carolinensis	10.2	0.188	10.2	0.188	White & Seymour $(2003)$
Insectivora	Soricidae	Crocidura crossei	9.5	0.117	9.8	0.121	Lovegrove (2003)
Insectivora	Soricidae	Crocidura crossei	10.2	0.125	20	0 121	White & Seymour (2003)
Insectivora	Soricidae	Crocidura flavescens	33.2	0.248	33.2	0.248	White & Seymour (2003)
Insectivora	Soricidae	Crocidura hildegardeae	10	0.145	10.7	0.156	White & Seymour (2003)
Insectivora	Soricidae	Crocidura hildegardeae	11.5	0.167	10 /	0 150	Lovegrove (2000)
Insectivora	Soricidae	Crocidura leucodon	11.7	0.166	11.7	0.166	Lovegrove (2003)
Insectivora	Soricidae	Crocidura luna	11.8	0.138	12.3	0.144	White & Seymour (2003)
Insectivora	Soricidae	Crocidura luna	12.8	0.150			Lovegrove (2000)
Insectivora	Soricidae	Crocidura olivieri	38.3	0.320	38.6	0.323	Lovegrove (2000)
Insectivora	Soricidae	Crocidura olivieri	38.9	0.326			White & Seymour (2003)
Insectivora	Soricidae	Crocidura poensis	16.9	0.170	17.1	0.172	Lovegrove (2000)
Insectivora	Soricidae	Crocidura poensis	17.3	0.173			White & Seymour (2003)
Insectivora	Soricidae	Crocidura russula	9.6	0.131	10.8	0.143	Lovegrove (2003)
Insectivora	Soricidae	Crocidura russula	10.1	0.166			Lovegrove (2000)
Insectivora	Soricidae	Crocidura russula	10.4	0.128			White & Seymour (2003)
Insectivora	Soricidae	Crocidura russula	13.7	0.150			Heusner (1991)
Insectivora	Soricidae	Crocidura suaveolens	6.5	0.105	6.9	0.112	White & Seymour (2003)
Insectivora	Soricidae	Crocidura suaveolens	6.8	0.110			Lovegrove (2003)
Insectivora	Soricidae	Crocidura suaveolens	7.5	0.120			Heusner (1991)
Insectivora	Soricidae	Crocidura viaria	14.7	0.123	15.0	0.126	White & Seymour (2003)
Insectivora	Soricidae	Crocidura viaria	15.3	0.128			Lovegrove (2000)
Insectivora	Soricidae	Cryptotis parva	6.2	0.107	6.3	0.164	White & Seymour (2003)
Insectivora	Soricidae	Cryptotis parva	6.4	0.250			Lovegrove (2000)
Insectivora	Soricidae	Neomys anomalus	13.1	0.373	13.1	0.373	White & Seymour (2003)
Insectivora	Soricidae	Neomys fodiens	14.1	0.373	16.0	0.328	Lovegrove (2000)
Insectivora	Soricidae	Neomys fodiens	17.1	0.310			Heusner (1991)
Insectivora	Soricidae	Neomys fodiens	17.1	0.305			White & Seymour (2003)
Insectivora	Soricidae	Notiosorex crawfordi	4	0.074	4.0	0.074	White & Seymour (2003)
Insectivora	Soricidae	Sorex alpinus	7.8	0.265	7.8	0.267	Lovegrove (2000)
Insectivora	Soricidae	Sorex alpinus	7.9	0.269	0.4	0.040	White & Seymour (2003)
Insectivora	Soricidae	Sorex araneus	8.05	0.336	8.4	0.348	White & Seymour (2003)
Insectivora	Soricidae	Sorex araneus	8.7	0.361	6.0	0.220	Lovegrove (2003)
Insectivora	Soricidae	Sorex cinereus	3.2	0.1/6	5.2	0.238	White & Seymour (2003)
Insectivora	Soricidae	Sorex cinereus	5	0.249			Lovegrove (2000)
Insectivora	Soricidae	Sorex cinereus	0.1	0.200	0.1	0.200	White & Source (2002)
Insectivora	Soricidae	Sorex coronalus	2.9	0.182	9·1	0.290	Lavagrava (2002)
Insectivora	Soricidae	Sorex minutus	2.9 V	0.172	4.1	0.179	White & Seymour (2002)
Insectivora	Soricidae	Sorex minutus	4	0.183			Lovegrove (2000)
Insectivora	Soricidae	Sorex minutus	4:2 1.6	0.180			Heusner (1991)
Insectivora	Soricidae	Sorex ornatus	9.7	0.202	9.7	0.292	White & Seymour (2003)
Insectivora	Soricidae	Sorex vagrans	5.2	0.157	5.2	0.157	White & Seymour (2003)
Insectivora	Soricidae	Suncus etruscus	2.4	0.080	2.4	0.063	White & Seymour (2003)
Insectivora	Soricidae	Suncus etruscus	2.5	0.050	∠ <del>1</del>	0.005	Heusner (1991)
Insectivora	Soricidae	Suncus murinus	30.2	0.332	39.7	0.403	White & Seymour (2003)
Insectivora	Soricidae	Suncus murinus	52.3	0.490	<i></i>		Heusner (1991)
Insectivora	Talpidae	Condylura cristata	49	0.615	49.0	0.615	White & Seymour (2003)

Order	Family	Species	Mass (g)	BMR (W)	Species avg. mass (g)	Species avg. BMR (W)	References
Insectivora	Talpidae	Neurotrichus gibbsii	11.8	0.259	11.8	0.259	White & Seymour (2003)
Insectivora	Talpidae	Scalopus aquaticus	48	0.378	48.0	0.378	White & Seymour (2003)
Insectivora	Talpidae	Scapanus latimanus	61	0.425	61.0	0.425	White & Seymour (2003)
Insectivora	Talpidae	Scapanus orarius	61.2	0.358	61.2	0.358	White & Seymour (2003)
Insectivora	Talpidae	Scapanus townsendii	130.1	0.607	130.1	0.607	Lovegrove (2000)
Insectivora	Tenrecidae	Echinops telfairi	116.4	0.750	116.4	0.750	Heusner (1991)
Insectivora	Tenrecidae	Geogale aurita	6.9	0.043	6.9	0.043	White & Seymour (2003)
Insectivora	Tenrecidae	Hemicentetes semispinosus	101.9	0.404	116.4	0.380	White & Seymour (2003)
Insectivora	Tenrecidae	Hemicentetes semispinosus	133	0.358			White & Seymour (2003)
Insectivora	Tenrecidae	Limnogale mergulus	77.7	0.312	77.7	0.355	White & Seymour (2003)
Insectivora	Tenrecidae	Limnogale mergulus	12.2	0.404	12.2	0.170	Lovegrove (2000)
Insectivora	Tenrecidae	Microgale cowani	12.2	0.1/9	12.2	0.1/9	White & Seymour (2003)
Insectivora	Tenrecidae	Microgale aobsoni	44.0	0.313	44.0	0.315	White & Seymour (2003)
Insectivora	Tenrecidae	Satifar satosus	345	0.483	44.0	0.243	L ovegrove (2000)
Insectivora	Tenrecidae	Setifer setosus	530	0.680	4270	0 575	White & Seymour (2003)
Insectivora	Tenrecidae	Toproc occudatus	650	0.729	650.0	0.729	White & Seymour (2003)
Lagomorpha	Leporidae	Brachylagus idahoensis	432	2.145	432.0	2.145	L ovegrove (2003)
Lagomorpha	Leporidae	Lenus alleni	3 000	9.205	3 200.4	9.220	White & Seymour (2003)
Lagomorpha	Leporidae	Lepus alleni	3 250	9.972	5 200 4	9 220	Lovegrove (2000)
Lagomorpha	Leporidae	Lepus alleni	3 362	8.540			Heusner (1991)
Lagomorpha	Leporidae	Lepus americanus	1 380	5.235	1 603.4	6.708	Hart (1971)
Lagomorpha	Leporidae	Lepus americanus	1 480	6.605	1 005 4	0 /00	Hart $(1971)$
Lagomorpha	Leporidae	Lepus americanus	1 562.8	6.975			Lovegrove (2000)
Lagomorpha	Leporidae	Lepus americanus	1 581	8.468			White & Seymour (2003)
Lagomorpha	Leporidae	Lepus americanus	2 100	6.650			Heusner (1991)
Lagomorpha	Leporidae	Lepus arcticus	3 004.4	6.036	3 004.4	6.036	White & Seymour (2003)
Lagomorpha	Leporidae	Lepus californicus	2 300	7.314	2 300.0	7.314	White & Seymour (2003)
Lagomorpha	Leporidae	Lepus timidus	3 004	6.033	3 014.5	8.443	Lovegrove (2000)
Lagomorpha	Leporidae	Lepus timidus	3 025	11.815	5 01 1 5	0 110	White & Seymour (2003)
Lagomorpha	Leporidae	Lepus townsendii	2 430	7.051	2 523.2	7.698	White & Seymour (2003)
Lagomorpha	Leporidae	Lepus townsendii	2 620	8.404		,	Lovegrove (2000)
Lagomorpha	Leporidae	Orvetolagus cuniculus	2 000	6.360	2167.9	7.395	White & Seymour (2003)
Lagomorpha	Leporidae	Oryctolagus cuniculus	2 350	8.600			Heusner (1991)
Lagomorpha	Leporidae	Svlvilagus audubonii	672.4	2.443	686.9	2.506	White & Seymour (2003)
Lagomorpha	Leporidae	Sylvilagus audubonii	701.7	2.570			Heusner (1991)
Lagomorpha	Ochotonidae	Ochotona dauurica	127.7	1.389	127.7	1.389	White & Seymour (2003)
Lagomorpha	Ochotonidae	Ochotona princeps	109	0.932	109.0	0.932	White & Seymour (2003)
Macroscelidae	Macroscelididae	Elephantulus brachyrhynchus	45.3	0.244	45.3	0.244	White & Seymour (2003)
Macroscelidae	Macroscelididae	Elephantulus edwardii	49.8	0.303	49.9	0.303	Lovegrove (2000)
Macroscelidae	Macroscelididae	Elephantulus edwardii	50	0.304			White & Seymour (2003)
Macroscelidae	Macroscelididae	Elephantulus intufi	46.49	0.290	46.5	0.290	White & Seymour (2003)
Macroscelidae	Macroscelididae	Elephantulus myurus	61	0.358	63.0	0.387	Lovegrove (2003)
Macroscelidae	Macroscelididae	Elephantulus myurus	62.97	0.370			White & Seymour (2003)
Macroscelidae	Macroscelididae	Elephantulus myurus	65.2	0.436			Lovegrove (2000)
Macroscelidae	Macroscelididae	Elephantulus rozeti	45.31	0.267	49.0	0.288	White & Seymour (2003)
Macroscelidae	Macroscelididae	Elephantulus rozeti	53	0.312			Lovegrove (2003)
Macroscelidae	Macroscelididae	Elephantulus rufescens	53	0.317	53.0	0.317	White & Seymour (2003)
Macroscelidae	Macroscelididae	Macroscelides proboscideus	39	0.292	39.0	0.292	White & Seymour (2003)
Macroscelidae	Macroscelididae	Petrodromus tetradactylus	206.1	1.001	208.0	0.852	Lovegrove (2003)
Macroscelidae	Macroscelididae	Petrodromus tetradactylus	208	0.859			Lovegrove (2000)
Macroscelidae	Macroscelididae	Petrodromus tetradactylus	210	0.720			Heusner (1991)
Monotremata	Ornithorhynchidae	Ornithorhynchus anatinus	693	1.082	1 030.3	1.931	White & Seymour (2003)
Monotremata	Ornithorhynchidae	Ornithorhynchus anatinus	1 200	2.500			Heusner (1991)
Monotremata	Ornithorynchidae	Ornithorhynchus anatinus	1 315	2.663			Lovegrove (2000)
Monotremata	Tachyglossidae	Tachyglossus aculeatus	2 140	1.564	2 909.0	2.327	Lovegrove (2000)
Monotremata	Tachyglossidae	Tachyglossus aculeatus	2 725	2.404			White & Seymour (2003)
Monotremata	Tachyglossidae	Tachyglossus aculeatus	3 430	2.550			Heusner (1991)
Monotremata	Tachyglossidae	Tachyglossus aculeatus	3 580	3.056			Lovegrove (2000)
Monotremata	Tachyglossidae	Zaglossus bruijni	10 300	6.778	11 848.6	6.493	White & Seymour (2003)
Monotremata	Tachyglossidae	Zaglossus bruijni	13 630	6.220			Heusner (1991)
Notoryctomorphia	Notoryctidae	Notoryctes caurinus	34	0.119	34.0	0.119	White & Seymour (2003)
Peramelemorphia	Peramelidae	Isoodon auratus	428	0.837	428.0	0.837	White & Seymour (2003)
Peramelemorphia	Peramelidae	Isoodon macrourus	1 551	3.202	1 551.0	3.202	white & Seymour (2003)
Peramelemorphia	Peramelidae	Isoodon obesulus	717	1.238	717.0	1.238	white & Seymour (2003)
Peramelemorphia	Peramelidae	Macrotis lagotis	1 011	1.974	1 245.5	2.400	Lovegrove (2000)
Peramelemorphia	Peramelidae	Macrotis lagotis	1 294	2.510			white & Seymour (2003)
Peramelemorphia	Peramelidae	Macrotis lagotis	1477	2.790	0.25.0	2.242	Heusner (1991)
Peramelemorphia	Peramelidae	Perametes gunnii	837	2.343	837.0	2.343	white & Seymour (2003)
Peramelemorphia	Peramendae	Ferameles nasuta	645	1.763	645.0	1./63	white & Seymour (2003)
Peramelemorphia	Peroryctidae	Ecnymipera rujescens	616	1.085	880.0	2.255	white & Seymour (2003)
Peramelemorphia	Peroryctidae	Ecnymipera rujescens	12/6	3.018	(05.0	1.000	white & Seymour (2003)
reramelemorphia	reroryctidae	rerametes gunnit	695	1.902	095.0	1.902	white & Seymour (2003)

Order	Family	Species	Mass (g)	BMR (W)	Species avg. mass (g)	Species avg. BMR (W)	References
Perissodactyla	Equidae	Equus asinus	177 500	164.920	177 500.0	164.920	Heusner (1991)
Pholidota	Manidae	Manis crassicaudata	15 910	6.923	15 910.0	6.923	White & Seymour (2003)
Pholidota	Manidae	Manis javanica	4 220	6.230	4 220.0	6.230	Heusner (1991)
Pholidota	Manidae	Manis pentadactyla	3 637.5	3.727	3 637.5	3.727	White & Seymour (2003)
Pholidota	Manidae	Manis tetradactyla	1 430	1.278	1 430.0	1.278	White & Seymour (2003)
Pholidota	Manidae	Manis tricuspis	1 365	1.540	1 930.4	2.670	White & Seymour (2003)
Pholidota	Manidae	Manis tricuspis	2 730	4.630	100.0	0.040	Heusner (1991)
Primates	Callitrichidae	Callithrix jacchus	190	0.848	190.0	0.848	White & Seymour (2003)
Primates Deimates	Callitrichidae	Callithrix pygmaea	105	0.550	110.7	0.599	Heusner (1991) White $\beta_{\rm c}$ Second even (2002)
Primates	Callitrichidae	Saguinus geoffrovi	225	1.305	225.0	1.305	White & Seymour (2003)
Primates	Cebidae	Alouatta palliata	4 670	11.464	4 670.0	11.464	White & Seymour (2003)
Primates	Cebidae	Actus trivirgatus	820	2.466	914.5	2.499	White & Seymour (2003)
Primates	Cebidae	Aotus trivirgatus	1 020	2.532	5115	2 100	Lovegrove (2000)
Primates	Cebidae	Saimiri sciureus	800	4.390	836.7	4.429	Heusner (1991)
Primates	Cebidae	Saimiri sciureus	875	4.468			White & Seymour (2003)
Primates	Cercopithecidae	Cercopithecus mitis	8 500	18.923	8 648.7	19.276	White & Seymour (2003)
Primates	Cercopithecidae	Cercopithecus mitis	8 800	19.637			Lovegrove (2000)
Primates	Cercopithecidae	Colobus guereza	10 450	16.613	10 623.6	17.037	White & Seymour (2003)
Primates	Cercopithecidae	Colobus guereza	10 800	17.472			Lovegrove (2000)
Primates	Cercopithecidae	Erythrocebus patas	3 000	5.958	3 000.0	5.958	White & Seymour (2003)
Primates	Cercopithecidae	Papio hamadryas	9 500	15.497	12 670.8	21.095	White & Seymour (2003)
Primates	Cercopithecidae	Papio hamadryas	16 900	28.713			White & Seymour (2003)
Primates	Cheirogaleidae	Cheirogaleus medius	300	1.088	300.0	1.088	White & Seymour (2003)
Primates	Hominidae	Homo sapiens sapiens	70 000	82.780	70 000.0	82.780	Heusner (1991)
Primates	Indrudae	Propithecus verreauxi	3 350	3.738	3 350.0	3.738	White & Seymour (2003)
Primates Deimates	Lemuridae	Eulemur Julvus	2 330	4.162	2 3/4.1	4.239	White & Seymour (2003)
Primates	Lemundae	Eulemur juivus	2 419	4.318	206.0	0.721	White & Sournour (2002)
Primates	Lorisidae	Fuotieus alagantulus	200	1.205	200.0	1.205	White & Seymour (2003)
Primates	Lorisidae	Galago moholi	170	0.285	170.0	0.285	White & Seymour (2003)
Primates	Lorisidae	Galago senegalensis	171.5	0.764	171.5	0.764	White & Seymour (2003)
Primates	Lorisidae	Galagoides demidoff	61	0.420	62.4	0.372	Heusner (1991)
Primates	Lorisidae	Galagoides demidoff	63.8	0.329			White & Seymour (2003)
Primates	Lorisidae	Loris tardigradus	284	0.714	284.0	0.714	White & Seymour (2003)
Primates	Lorisidae	Nycticebus coucang	953.3	1.292	1 128.6	1.504	Lovegrove (2000)
Primates	Lorisidae	Nycticebus coucang	1 160	1.523			White & Seymour (2003)
Primates	Lorisidae	Nycticebus coucang	1 300	1.730			Heusner (1991)
Primates	Lorisidae	Otolemur crassicaudatus	950	2.298	993.5	2.595	White & Seymour (2003)
Primates	Lorisidae	Otolemur crassicaudatus	1 039	2.930			Heusner (1991)
Primates	Lorisidae	Otolemur garnettii	1 314	3.927	1 314.0	3.927	White & Seymour (2003)
Primates	Lorisidae	Perodicticus potto	932.5	1.940	968.6	1.942	Lovegrove (2000)
Primates Deimates	Lorisidae	Perodicticus potto	964	1.824			White & Seymour (2003)
Primates	Tornsidae	Terroliciicus polito	1 011	2.070	172.0	0.921	White & Source our (2002)
Primates	Tarsiidae	Tarsius spectrum Tarsius sprichta	173	0.430	113.0	0.430	White & Seymour (2003)
Proboscidea	Elphantidae	Elephas maximus	3 672 000	2336.500	3 672 000.0	2336.500	Heusper (1991)
Rodentia	Agoutidae	Agouti paca	9 1 5 6	15:323	9 156.0	15.323	White & Seymour (2003)
Rodentia	Aplodontidae	Aplodontia rufa	630	1.546	706.8	1.892	White & Seymour (2003)
Rodentia	Aplodontidae	Aplodontia rufa	793	2.314			Lovegrove (2000)
Rodentia	Bathyergidae	Bathyergus janetta	406	1.201	406.0	1.201	White & Seymour (2003)
Rodentia	Bathyergidae	Bathyergus suillus	620	1.695	664.4	1.798	White & Seymour (2003)
Rodentia	Bathyergidae	Bathyergus suillus	712	1.907			Lovegrove (2000)
Rodentia	Bathyergidae	Cryptomys bocagei	94	0.388	94.0	0.388	White & Seymour (2003)
Rodentia	Bathyergidae	Cryptomys damarensis	125	0.397	131.3	0.418	Lovegrove (2000)
Rodentia	Bathyergidae	Cryptomys damarensis	138	0.439			White & Seymour (2003)
Rodentia	Bathyergidae	Cryptomys hottentotus	60	0.328	78.9	0.350	Lovegrove (2000)
Rodentia	Bathyergidae	Cryptomys hottentotus	71	0.380			Heusner (1991)
Rodentia	Bathyergidae	Cryptomys hottentotus	/5	0.377			White & Seymour (2003)
Rodentia	Bathyergidae	Cryptomys hottentotus	//	0.271			Lovegrove (2000)
Rodentia	Bathyergidae	Cryptomys nottentotus	/9.5	0.310			L avagrava (2000)
Rodentia	Bathyorgidae	Cryptomys hottentotus	93	0.455			White & Sournour (2002)
Rodentia	Bathyergidae	Cryptomys notientotus	267	0.433	260.5	0.902	White & Seymour (2003)
Rodentia	Bathyergidae	Cryptomys mechowi Cryptomys mechowi	207	0.910	207 5	0 902	Lovegrove (2000)
Rodentia	Bathyergidae	Georvchus canensis	191	0.679	193.0	0.637	Lovegrove (2000)
Rodentia	Bathyergidae	Georychus capensis	195	0.645	175 0	0.007	White & Seymour (2003)
Rodentia	Bathyergidae	Heliophobius argenteocinereus	88	0.420	88.5	0.430	Heusner (1991)
Rodentia	Bathyergidae	Heliophobius argenteocinereus	89	0.440	000		Heusner (1991)
Rodentia	Bathyergidae	Heterocephalus glaber	32	0.114	35.3	0.128	White & Seymour (2003)
Rodentia	Bathyergidae	Heterocephalus glaber	39	0.144			Lovegrove (2000)
Rodentia	Capromyidae	Capromys pilorides	2 630	3.375	2 630.0	3.375	White & Seymour (2003)
Rodentia	Capromyidae	Geocapromys brownii	2 456	4.110	2 456.0	4.110	White & Seymour (2003)

Order	Family	Species	Mass (g)	BMR (W)	Species avg. mass (g)	Species avg. BMR (W)	References
Rodentia	Capromyidae	Geocapromys ingrahami	775	1.483	775.0	1.483	White & Seymour (2003)
Rodentia	Caviidae	Cavia porcellus	570	2.226	639.1	2.130	Hart (1971)
Rodentia	Caviidae	Cavia porcellus	629	1.930			White & Seymour (2003)
Rodentia	Caviidae	Cavia porcellus	728	2.250	1 (12 0	4.050	Heusner (1991)
Rodentia	Caviidae	Dolichotis salinicola	1 613	4.050	1 613.0	4.050	White & Seymour (2003)
Rodentia	Caviidae	Galea musielolaes Karodon runastris	322 801	2.011	322·0 801:0	2.011	White & Seymour (2003)
Rodentia	Caviidae	Microcavia niata	255	0.980	255.0	0.980	White & Seymour (2003)
Rodentia	Chinchillidae	Chinchilla lanigera	403	1.574	436.7	1.310	Lovegrove (2000)
Rodentia	Chinchillidae	Chinchilla lanigera	426	1.117			White & Seymour (2003)
Rodentia	Chinchillidae	Chinchilla lanigera	485	1.280			Heusner (1991)
Rodentia	Chinchillidae	Lagostomus maximus	6 784	10.597	6 794·0	10.623	Lovegrove (2000)
Rodentia	Chinchillidae	Lagostomus maximus	6 804	10.650			Heusner (1991)
Rodentia	Ctenomyidae	Ctenomys australis	340	0.650	340.0	0.650	White & Seymour (2003)
Rodentia	Ctenomyidae	Ctenomys fulvus	300	1.054	300.0	1.054	White & Seymour (2003)
Rodentia	Ctenomyidae	Ctenomys maulinus	215	1.044	215.0	1.044	White & Seymour (2003)
Rodentia	Ctenomyidae	Ctenomys peruanus Ctenomys talarum	490	0.611	490.0	0.611	White & Seymour (2003)
Rodentia	Dasyproctidae	Dasvprocta azarae	3 849	10.521	3 849.0	10.521	White & Seymour (2003)
Rodentia	Dasyproctidae	Dasyprocta leporina	2 687	8.694	2 687.0	8.694	White & Seymour (2003)
Rodentia	Dasyproctidae	Myoprocta acouchy	914	2.804	914·0	2.804	White & Seymour (2003)
Rodentia	Dipodidae	Dipus sagitta?	160	0.676	160.0	0.676	White & Seymour (2003)
Rodentia	Dipodidae	Jaculus jaculus	75	0.515	75.0	0.515	White & Seymour (2003)
Rodentia	Dipodidae	Jaculus orientalis	139	0.775	139.0	0.775	White & Seymour (2003)
Rodentia	Dipodidae	Napaeozapus insignis	21.6	0.220	21.8	0.220	Heusner (1991)
Rodentia	Dipodidae	Napaeozapus insignis	22	0.221			White & Seymour (2003)
Rodentia	Dipodidae	Sicista betulina	10	0.179	10.0	0.179	White & Seymour (2003)
Rodentia	Dipodidae	Zapus hudsonius	23.8	0.199	26.1	0.219	White & Seymour (2003)
Rodentia	Dipodidae	Zapus hudsonius	25	0.209			Hart (1971)
Rodentia	Dipodidae	Zapus hudsonius	30	0.251	408.0	1 750	Lovegrove (2000)
Rodentia	Echimyidae	Thrichomys aparaoidas	490	1.153	498.0	1.153	White & Seymour (2003)
Rodentia	Erethizontidae	Coendou prehensilis	3 280	5.123	3 280.0	5.123	White & Seymour (2003)
Rodentia	Erethizontidae	Erethizon dorsatum	4 290	11.966	6 871·0	13.675	Hart (1971)
Rodentia	Erethizontidae	Erethizon dorsatum	6 790	13.760			Heusner (1991)
Rodentia	Erethizontidae	Erethizon dorsatum	11 136	15.531			White & Seymour (2003)
Rodentia	Geomyidae	Geomys bursarius	197	0.769	197.0	0.769	Bradley & Yousef (1975)
Rodentia	Geomyidae	Geomys pinetis	173	0.743	191.5	0.768	White & Seymour (2003)
Rodentia	Geomyidae	Geomys pinetis	200	0.792			Lovegrove (2000)
Rodentia	Geomyidae	Geomys pinetis	203	0.770			Heusner (1991)
Rodentia	Geomyidae	Thomomys bottae	143	0.670	143.0	0.670	White & Seymour (2003)
Rodentia	Geomyidae	Thomomys talpoides	82.0	0.550	97.6	0.679	Heusner (1991)
Rodentia	Geomyidae	Thomomys talpoides	105.5	0.792			White & Seymour (2003)
Rodentia	Geomyidae	Thomomys umbrinus	85	0.403	90.0	0.427	White & Seymour (2003)
Rodentia	Geomyidae	Thomomys umbrinus	95.3	0.452	20.0	0 127	Lovegrove (2000)
Rodentia	Heteromyidae	Chaetodipus bailevi	29.1	0.192	29.1	0.192	White & Seymour (2003)
Rodentia	Heteromyidae	Chaetodipus californicus	22	0.119	22.0	0.119	White & Seymour (2003)
Rodentia	Heteromyidae	Chaetodipus fallax	19.6	0.150	19.6	0.150	Hinds & MacMillen (1985)
Rodentia	Heteromyidae	Chaetodipus formosus	15.1	0.103	15.1	0.103	Lovegrove (2003)
Rodentia	Heteromyidae	Chaetodipus hispidus	32	0.256	35.6	0.266	Lovegrove (2003)
Rodentia	Heteromyidae	Chaetodipus hispidus	35.8	0.268			Lovegrove (2000)
Rodentia	Heteromyidae	Chaetodipus hispidus	39.5	0.276	15.0	0.107	White & Seymour (2003)
Rodentia	Heteromyidae	Chaeto dinus intermedius	14.0	0.100	15.9	0.106	Lovegrove (2000) White & Sourneyur (2002)
Rodentia	Heteromyidae	Chaetodipus intermedius	13	0.136			L ovegrove (2003)
Rodentia	Heteromyidae	Chaetodipus mericillatus	16 5	0.125	16.0	0.125	White & Seymour (2003)
Rodentia	Heteromyidae	Dipodomys agilis	60.6	0.355	60.6	0.355	White & Seymour (2003)
Rodentia	Heteromyidae	Dipodomys deserti	104.7	0.541	105.8	0.517	Lovegrove (2003)
Rodentia	Heteromyidae	Dipodomys deserti	104.9	0.524			Lovegrove (2000)
Rodentia	Heteromyidae	Dipodomys deserti	106	0.514			White & Seymour (2003)
Rodentia	Heteromyidae	Dipodomys deserti	107.5	0.490			Heusner (1991)
Rodentia	Heteromyidae	Dipodomys heermanni	63.3	0.408	63.3	0.408	White & Seymour (2003)
Rodentia	Heteromyidae	Dipodomys merriami	35	0.234	37.6	0.246	Hart (1971)
Rodentia	Heteromyidae	Dipodomys merriami	35.8	0.295			Lovegrove (2003)
Rodentia	Heteromyidae	Dipodomys merriami	36.5	0.237			White & Seymour (2003)
Rodentia	Heteromyidae	Dipodomys merriami	3/./	0.248			Lovegrove (2000)
Rodentia	Heteromyidaa	Dipodomys merriami	38 42.4	0.240			11a11 (17/1) Heisner (1001)
Rodentia	Heteromyidae	Dipodomys merriami	45.4	0.200	54.6	0.335	Lovegrove (2003)
Rodentia	Heteromvidae	Dipodomys microps Dipodomys microps	54.2	0.330	54.0	0 555	Heusner (1991)
Rodentia	Heteromyidae	Dipodomys microps	55.7	0.336			Lovegrove (2000)
Rodentia	Heteromyidae	Dipodomys microps	57.2	0.373			White & Seymour (2003)

Order	Family	Species	Mass (g)	BMR (W)	Species avg. mass (g)	Species avg. BMR (W)	References
Rodentia	Heteromyidae	Dipodomys nitratoides	37.8	0.257	37.8	0.204	White & Seymour (2003)
Rodentia	Heteromyidae	Dipodomys nitratoides	37.8	0.162			Lovegrove (2003)
Rodentia	Heteromyidae	Dipodomys ordii	46.8	0.358	47.8	0.339	White & Seymour (2003)
Rodentia	Heteromyidae	Dipodomys ordii	48.8	0.320	(0.4	0.207	Heusner (1991)
Rodentia	Heteromyidae	Dipodomys panamintinus	56.9	0.380	60.4	0.397	Heusner (1991) White & Saumour (2002)
Rodentia	Heteromyidae	Heteromys anomalus	69.3	0.414	69.3	0.561	White & Seymour (2003)
Rodentia	Heteromyidae	Heteromys desmarestianus	75.8	0.553	75.8	0.553	White & Seymour (2003) White & Seymour (2003)
Rodentia	Heteromyidae	Liomys irroratus	44.9	0.336	46.5	0.318	Lovegrove (2003)
Rodentia	Heteromyidae	Liomys irroratus	48.1	0.301			White & Seymour (2003)
Rodentia	Heteromyidae	Liomys salvini	42.7	0.313	43.7	0.281	Lovegrove (2003)
Rodentia	Heteromyidae	Liomys salvini	43.8	0.262			White & Seymour (2003)
Rodentia	Heteromyidae	Liomys salvini	44.5	0.270	11.0	0.1.00	Lovegrove (2000)
Rodentia	Heteromyidae	Microdipodops megacephalus Microdino dona nallidua	11	0.110	11.0	0.110	White & Seymour (2003)
Rodentia	Heteromyidae	Microalpodops pailidus Parognathus flavus	8.3	0.097	8.3	0.097	White & Seymour (2003)
Rodentia	Heteromyidae	Perognathus Jangimembris	8.2	0.020	8.5	0.061	Lovegrove (2000)
Rodentia	Heteromyidae	Perognathus longimembris	8.9	0.053	0.5	0 001	White & Seymour (2003)
Rodentia	Heteromyidae	Perognathus parvus	19.2	0.160	19.2	0.160	Heusner (1991)
Rodentia	Hydrochaeridae	Hydrochaeris hydrochaeris	26 385	36.798	26 385.0	36.798	White & Seymour (2003)
Rodentia	Hystricidae	Hystrix africaeaustralis	11 300	13.175	11 300.0	13.175	White & Seymour (2003)
Rodentia	Muridae	Acomys cahirinus	42	0.258	42.0	0.258	White & Seymour (2003)
Rodentia	Muridae	Acomys russatus	51.1	0.230	55.4	0.240	Heusner (1991)
Rodentia	Muridae	Acomys russatus	55.55	0.239			White & Seymour (2003)
Rodentia	Muridae	Acomys russatus	60 27.02	0.251	27.0	0.246	Lovegrove (2003) White & Saumour (2002)
Rodentia	Muridae	Acomys spinosissimus	32.25	0.465	27.0	0.465	White & Seymour (2003)
Rodentia	Muridae	Aethomys namaauensis	57.3	0.269	62.6	0.292	Lovegrove (2000)
Rodentia	Muridae	Aethomys namaquensis	64·2	0.317	02.0	0 272	White & Seymour (2003)
Rodentia	Muridae	Aethomys namaquensis	66.6	0.293			Lovegrove (2003)
Rodentia	Muridae	Akodon albiventer	31	0.259	31.0	0.259	White & Seymour (2003)
Rodentia	Muridae	Akodon azarae	23.5	0.223	23.7	0.225	Lovegrove (2000)
Rodentia	Muridae	Akodon azarae	24	0.228			White & Seymour (2003)
Rodentia	Muridae	Akodon lanosus	24	0.254	24.0	0.254	White & Seymour (2003)
Rodentia	Muridae	Akodon longipilis	42.3	0.321	42.3	0.321	White & Seymour (2003)
Rodentia	Muridae	Akodon olivaceus	27	0.675	27.0	0.675	White & Seymour (2003)
Rodentia	Muridae	Anicola argenialas Anodemus agrarius	21.2	0.373	21.2	0.373	L ovegrove (2003)
Rodentia	Muridae	Apodemus flavicollis	23.4	0.236	28.3	0.365	Lovegrove (2003)
Rodentia	Muridae	Apodemus flavicollis	23.9	0.242			White & Seymour (2003)
Rodentia	Muridae	Apodemus flavicollis	40.5	0.850			Lovegrove (2000)
Rodentia	Muridae	Apodemus hermonensis	20.5	0.279	20.6	0.280	White & Seymour (2003)
Rodentia	Muridae	Apodemus hermonensis	20.7	0.282			Lovegrove (2000)
Rodentia	Muridae	Apodemus mystacinus	40.4	0.312	41.3	0.351	White & Seymour (2003)
Rodentia	Muridae	Apodemus mystacinus	42.3	0.394	22.9	0.264	Lovegrove (2000)
Rodentia	Muridae	Apodemus sylvaticus	22	0.242	23.8	0.204	White & Seymour (2003)
Rodentia	Muridae	Apodemus sylvaticus Anodemus sylvaticus	25.7	0.242			Lovegrove (2003)
Rodentia	Muridae	Arborimus longicaudus	21.8	0.329	21.8	0.329	White & Seymour (2003)
Rodentia	Muridae	Arvicola terrestris	92	0.595	94.7	0.613	White & Seymour (2003)
Rodentia	Muridae	Arvicola terrestris	97.5	0.631			Lovegrove (2000)
Rodentia	Muridae	Auliscomys boliviensis	76.8	0.617	76.8	0.617	White & Seymour (2003)
Rodentia	Muridae	Auliscomys micropus	62.3	0.546	62.3	0.546	White & Seymour (2003)
Rodentia	Muridae	Baiomys taylori	7.15	0.095	7.2	0.095	White & Seymour (2003)
Rodentia	Muridae	Calomys callosus	48	0.305	49.2	0.3/1	Lovegrove (2000)
Rodentia	Muridae	Calomys callosus	50.1	0.417			White & Seymour (2003)
Rodentia	Muridae	Calomys lepidus	16	0.161	16.0	0.161	Lovegrove (2003)
Rodentia	Muridae	Calomys musculinus	16.9	0.154	16.9	0.154	White & Seymour (2003)
Rodentia	Muridae	Cannomys badius	344	0.960	344.0	0.960	White & Seymour (2003)
Rodentia	Muridae	Chionomys nivalis	32.8	0.452	32.8	0.452	White & Seymour (2003)
Rodentia	Muridae	Chroeomys andinus	34.6	0.361	34.7	0.353	White & Seymour (2003)
Rodentia	Muridae	Chroeomys andinus	34.9	0.345	10.0		Lovegrove (2003)
Rodentia	Muridae	Clethrionomys californicus	18.3	0.341	18.3	0.341	Lovegrove (2000) White & Saverana (2002)
Rodentia	Muridae	Clethrionomys gapperi	22.3	0.275	23.4	0.291	white & Seymour (2003)
Rodentia	Muridae	Clethrionomys gapperi	23°3 24.6	0.270			Lovegrove (2005)
Rodentia	Muridae	Clethrionomys gappen Clethrionomys glareolus	18	0.311	21.5	0.312	Hart (1971)
Rodentia	Muridae	Clethrionomys glareolus	20.5	0.270	21.5	0.512	Heusner (1991)
Rodentia	Muridae	Clethrionomys glareolus	23.4	0.354			White & Seymour (2003)
Rodentia	Muridae	Clethrionomys glareolus	24.6	0.320			Lovegrove (2003)
Rodentia	Muridae	Clethrionomys rufocanus	27	0.331	27.2	0.321	White & Seymour (2003)
Rodentia	Muridae	Clethrionomys rufocanus	27.5	0.310			Heusner (1991)

Order	Family	Species	Mass (g)	BMR (W)	Species avg. mass (g)	Species avg. BMR (W)	References
Rodentia	Muridae	Clethrionomys rutilus	28	0.430	28.0	0.430	White & Seymour (2003)
Rodentia	Muridae	Conilurus penicillatus	213.2	0.908	213.2	0.908	White & Seymour (2003)
Rodentia	Muridae	Cricetomys gambianus	1 521.4	5.703	1 686.7	6.024	Lovegrove (2000)
Rodentia	Muridae	Cricetomys gambianus	1 870	6·364	20.7	0.245	White & Seymour (2003)
Rodentia	Muridae	Cricetulus migratorius	30.7	0.245	30.7	0.245	White & Seymour (2003)
Rodentia	Muridae	Cricetus cricetus	362	1.293	505.5	1.7231	White & Seymour (2003)
Rodentia	Muridae	Cricetus cricetus	400	1.272			Hart (1971)
Rodentia	Muridae	Desmodillus auricularis	71.93	0.490	71.9	0.490	White & Seymour (2003)
Rodentia	Muridae	Dicrostonyx groenlandicus	47	0.520	56.8	0.459	Heusner (1991)
Rodentia	Muridae	Dicrostonyx groenlandicus	59.62	0.551			White & Seymour (2003)
Rodentia	Muridae	Dicrostonyx groenlandicus	61	0.391			Hart (1971)
Rodentia	Muridae	Dicrostonyx groenlandicus	61	0.395			Hart (1971)
Rodentia	Muridae	Eligmodontia typus	17.5	0.167	17.5	0.167	White & Seymour (2003)
Rodentia	Muridae	Euneomys chinchilloides	65·4 22.0	0.4/1	65·4 22.0	0.104	White & Seymour (2003) White & Saymour (2003)
Rodentia	Muridae	Gerbillurus setzeri	46.1	0.206	46.1	0.206	White & Seymour (2003)
Rodentia	Muridae	Gerbillurus tytonis	29.9	0.177	29.9	0.177	White & Seymour (2003)
Rodentia	Muridae	Gerbillurus vallinus	38.8	0.194	38.8	0.194	White & Seymour (2003)
Rodentia	Muridae	Gerbillus allenbyi	35.3	0.217	35.3	0.217	Lovegrove (2000)
Rodentia	Muridae	Gerbillus dasyurus	27.6	0.163	27.6	0.163	White & Seymour (2003)
Rodentia	Muridae	Gerbillus gerbillus	29.7	0.237	29.7	0.237	White & Seymour (2003)
Rodentia	Muridae	Gerbillus nanus	28.4	0.124	29.7	0.129	White & Seymour (2003)
Rodentia	Muridae	Gerbillus nanus	31	0.135			Lovegrove (2000)
Rodentia	Muridae	Gerbillus perpallidus	52.4	0.243	56.3	0.261	White & Seymour (2003)
Rodentia	Muridae	Gerbillus perpallidus	60.5	0.280	12.0	0.075	Lovegrove (2003)
Rodentia	Muridae	Gerbillus pusillus	12.0	0.075	12.6	0.075	White & Seymour (2003)
Rodentia	Muridae	Gerbuius pyramaum Golunda ellioti	56.2	0.330	108.3	0.330	Lovegrove (2003)
Rodentia	Muridae	Graomys griseoflavus	69·4	0.469	69·4	0.469	White & Seymour (2003)
Rodentia	Muridae	Hydromys chrysogaster	900	2.970	900.0	2.970	Heusner (1991)
Rodentia	Muridae	Isthmomys pirrensis	137.9	0.677	137.9	0.677	White & Seymour (2003)
Rodentia	Muridae	Lasiopodomys brandtii	40.2	0.428	40.2	0.428	White & Seymour (2003)
Rodentia	Muridae	Lemmiscus curtatus	30.3	0.281	30.3	0.281	White & Seymour (2003)
Rodentia	Muridae	Lemmus lemmus	80	1.071	80.0	1.071	White & Seymour (2003)
Rodentia	Muridae	Lemmus sibiricus	50.2	0.503	60.8	0.667	White & Seymour (2003)
Rodentia	Muridae	Lemmus sibiricus	64	0.882			Lovegrove (2000)
Rodentia	Muridae	Lemmus sibiricus	70	0.670	47.5	0.221	Heusner (1991)
Rodentia	Muridae	Lemniscomys griselda	4/.5	0.321	4/.5	0.321	White & Seymour (2003) White & Saymour (2003)
Rodentia	Muridae	Malacothrix typica	21.7	0.115	21.7	0.115	White & Seymour (2003)
Rodentia	Muridae	Mastomys natalensis	41.49	0.183	41.5	0.183	Lovegrove (2000)
Rodentia	Muridae	Megadontomys thomasi	110.8	0.692	110.8	0.692	White & Seymour (2003)
Rodentia	Muridae	Meriones hurrianae	69	0.304	70.6	0.301	White & Seymour (2003)
Rodentia	Muridae	Meriones hurrianae	72.3	0.298			Lovegrove (2003)
Rodentia	Muridae	Meriones tristrami	112	0.550	112.0	0.550	White & Seymour (2003)
Rodentia	Muridae	Meriones unguiculatus	58.1	0.690	64.8	0.546	Lovegrove (2003)
Rodentia	Muridae	Meriones unguiculatus	67	0.430			White & Seymour (2003)
Rodentia	Muridae	Meriones unguiculatus	70	0.547	100.0	0.000	Hart (1971)
Rodentia	Muridae	Mesocricelus auralus	98	0.820	108-2	0.690	White & Seymour (2003)
Rodentia	Muridae	Micromys minutus	6	0.224	7.6	0.201	Hart $(1971)$
Rodentia	Muridae	Micromys minutus	7.37	0.118	, 0	0 201	White & Seymour (2003)
Rodentia	Muridae	Micromys minutus	8.7	0.240			Heusner (1991)
Rodentia	Muridae	Micromys minutus	8.71	0.260			Heusner (1991)
Rodentia	Muridae	Microtus agrestis	22.3	0.380	25.0	0.367	Heusner (1991)
Rodentia	Muridae	Microtus agrestis	28	0.355			White & Seymour (2003)
Rodentia	Muridae	Microtus arvalis	20	0.346	21.9	0.343	White & Seymour (2003)
Rodentia	Muridae	Microtus arvalis	23.9	0.340	50 I		Heusner (1991)
Rodentia	Muridae	Microtus breweri	53.1	0.412	53-1	0.412	White & Seymour (2003)
Rodentia	Muridae	Microtus californicus Microtus cucathoni	44	0.380	44.0	0.380	White & Seymour (2003)
Rodentia	Muridae	Microtus longicandus	28.6	0.377	43.8	0.383	White & Seymour (2003)
Rodentia	Muridae	Microtus longicaudus	30.2	0.347	52 5	0 505	Lovegrove (2003)
Rodentia	Muridae	Microtus longicaudus	31.2	0.410			Lovegrove (2000)
Rodentia	Muridae	Microtus longicaudus	41.4	0.400			Heusner (1991)
Rodentia	Muridae	Microtus mexicanus	28	0.260	28.4	0.261	Heusner (1991)
Rodentia	Muridae	Microtus mexicanus	28.8	0.262			White & Seymour (2003)
Rodentia	Muridae	Microtus montanus	30.8	0.455	32.9	0.460	Lovegrove (2000)
Rodentia	Muridae	Microtus montanus	35.1	0.465			White & Seymour (2003)
Rodentia	Muridae	Microtus ochrogaster	46.7	0.441	48.2	0.410	White & Seymour (2003)
Rodentia	Muridae	Microtus ochrogaster	4/	0.240			Lovegrove (2000)
кодениа	wiuridae	MICrotus ochrogaster	51	0.340			neusner (1991)

Order	Family	Species	Mass (g)	BMR (W)	Species avg. mass (g)	Species avg. BMR (W)	References
Rodentia	Muridae	Microtus oeconomus	32	0.570	32.8	0.566	Heusner (1991)
Rodentia	Muridae	Microtus oeconomus	33.7	0.563			White & Seymour (2003)
Rodentia	Muridae	Microtus pennsylvanicus	37.8	0.457	38.2	0.428	Lovegrove (2000)
Rodentia	Muridae	Microtus pennsylvanicus	38	0.410			Heusner (1991)
Rodentia	Muridae	Microtus pennsylvanicus Microtus pinctorum	38.9	0.212	24.8	0.205	Unite & Seymour (2003)
Rodentia	Muridae	Microtus pinetorum	25'8	0.280	24.0	0.303	Heusner (1991)
Rodentia	Muridae	Microtus pinetorum	25·5	0.326			White & Seymour (2003)
Rodentia	Muridae	Microtus richardsoni	51	0.500	64.5	0.701	Heusner (1991)
Rodentia	Muridae	Microtus richardsoni	65.65	0.714			White & Seymour (2003)
Rodentia	Muridae	Microtus richardsoni	80	0.964			Lovegrove (2003)
Rodentia	Muridae	Microtus subterraneus	17.8	0.276	17.8	0.276	White & Seymour (2003)
Rodentia	Muridae	Microtus townsendii	52-2	0.504	52.2	0.504	White & Seymour (2003)
Rodentia	Muridae	Milcrolus xanthognathus Millardia maltada	68·5	0.337	68·5 67.4	0.327	White & Seymour (2003)
Rodentia	Muridae	Mus minutoides	7.92	0.124	8.0	0.129	L ovegrove (2000)
Rodentia	Muridae	Mus minutoides	8.06	0.134	00	0 12)	White & Seymour (2003)
Rodentia	Muridae	Mus musculus	13.2	0.365	18.0	0.271	Lovegrove (2003)
Rodentia	Muridae	Mus musculus	17	0.160			Heusner (1991)
Rodentia	Muridae	Mus musculus	26	0.340			Heusner (1991)
Rodentia	Muridae	Mus spretus	21.8	0.345	21.8	0.345	White & Seymour (2003)
Rodentia	Muridae	Myopus schisticolor	26.4	0.522	26.4	0.522	White & Seymour (2003)
Rodentia	Muridae	Mystromys albicaudatus	93.78	0.707	93.8	0.707	White & Seymour (2003)
Rodentia	Muridae	Nannospalax ehrenbergi	128	0.614	133.8	0.585	Lovegrove (2000)
Rodentia	Muridae	Nannospalax ehrenbergi	134	0.568			White & Seymour (2003)
Rodentia	Muridae	Nannospalax ehrenbergi	134	0.462			White & Seymour (2003)
Rodentia	Muridae	Nannospalax ehrenbergi	133	0.662			White & Seymour (2003)
Rodentia	Muridae	Nannospalax leucodon	151.9	0.002	183.3	0.760	Lovegrove (2000)
Rodentia	Muridae	Nannospalax leucodon	177.9	0.630	105 5	0 / 00	Heusner (1991)
Rodentia	Muridae	Nannospalax leucodon	201	0.830			White & Seymour (2003)
Rodentia	Muridae	Nannospalax leucodon	208	0.893			Hart (1971)
Rodentia	Muridae	Neofiber alleni	258.1	1.209	258.1	1.209	White & Seymour (2003)
Rodentia	Muridae	Neotoma albigula	172.4	0.720	177.6	0.735	Heusner (1991)
Rodentia	Muridae	Neotoma albigula	183	0.750			White & Seymour (2003)
Rodentia	Muridae	Neotoma cinerea	205.1	0.941	256.5	1.152	White & Seymour (2003)
Rodentia	Muridae	Neotoma cinerea	320.9	1.410	197.0	0.824	Heusner (1991) White & Savenaur (2002)
Rodentia	Muridae	Neotoma Juscipes	08.7	0.413	187.0	0.460	L ovegrove (2003)
Rodentia	Muridae	Neotoma lepida	106	0.360	112 5	0 400	Heusner (1991)
Rodentia	Muridae	Neotoma lepida	110	0.485			White & Seymour (2003)
Rodentia	Muridae	Neotoma lepida	113.4	0.517			Lovegrove (2000)
Rodentia	Muridae	Neotoma lepida	138	0.554			Hart (1971)
Rodentia	Muridae	Notomys alexis	32.3	0.252	32.3	0.252	White & Seymour (2003)
Rodentia	Muridae	Notomys cervinus	33.2	0.246	33.7	0.239	Lovegrove (2000)
Rodentia	Muridae	Notomys cervinus	34.2	0.233	10.5		White & Seymour (2003)
Rodentia	Muridae	Ochrotomys nuttalli	19.5	0.151	19.5	0.151	White & Seymour (2003)
Rodentia	Muridae	Ongoryzomys longicauaatus	28.2	2.800	28.2	0.285	Houspor (1991)
Rodentia	Muridae	Ondatra zibethicus	1 004.6	3.586	570 5	4 505	White & Seymour (2003)
Rodentia	Muridae	Ondatra zibethicus	1 100	5.952			Hart (1971)
Rodentia	Muridae	Onychomys torridus	19.1	0.165	19.1	0.165	White & Seymour (2003)
Rodentia	Muridae	Otomys irroratus	102	0.474	102.0	0.474	White & Seymour (2003)
Rodentia	Muridae	Otomys sloggetti	113.29	0.746	113.3	0.746	White & Seymour (2003)
Rodentia	Muridae	Otomys unisulcatus	96	0.595	96.0	0.595	White & Seymour (2003)
Rodentia	Muridae	Oxymycterus roberti	83.5	0.508	83.5	0.508	White & Seymour (2003)
Rodentia	Muridae	Parotomys brantsii	86.5	0.468	86.5	0.468	White & Seymour (2003)
Rodentia	Muridae	Peromyscus boylii Peromyscus agliforniaus	23.2	0.303	23.2	0.303	Unite & Seymour (2003)
Rodentia	Muridae	Peromyscus californicus	47.6	0.201	47.0	0.201	White & Seymour (2003)
Rodentia	Muridae	Peromyscus californicus	48	0.250			Heusner (1991)
Rodentia	Muridae	Peromyscus crinitus	13.6	0.100	20.5	0.162	Heusner (1991)
Rodentia	Muridae	Peromyscus crinitus	15.9	0.140			Lovegrove (2003)
Rodentia	Muridae	Peromyscus crinitus	16	0.143			Hart (1971)
Rodentia	Muridae	Peromyscus crinitus	20.9	0.173			Lovegrove (2003)
Rodentia	Muridae	Peromyscus crinitus	49.6	0.324			White & Seymour (2003)
Rodentia	Muridae	Peromyscus eremicus	20	0.179	21.0	0.173	Hart (1971)
Rodentia	Muridae	Peromyscus eremicus	20.7	0.195			Heusner (1991) White & Saver and (2002)
Rodentia	Muridae	reromyscus eremicus Peromyscus eremicus	21.5	0.185			Ville & Seymour (2003)
Rodentia	Muridae	Peromyscus eremicus	22	0.102	21.5	0.206	White & Sevmour (2003)
Rodentia	Muridae	Peromyscus leucopus	20	0.185	22.3	0.213	White & Seymour (2003)
Rodentia	Muridae	Peromyscus leucopus	21.4	0.189		ŕ	Lovegrove (2000)

Order	Family	Species	Mass (g)	BMR (W)	Species avg. mass (g)	Species avg. BMR (W)	References
Rodentia	Muridae	Peromyscus leucopus	22.1	0.205			Lovegrove (2003)
Rodentia	Muridae	Peromyscus leucopus	22.3	0.190			Heusner (1991)
Rodentia	Muridae	Peromyscus leucopus	26	0.319			Hart (1971)
Rodentia	Muridae	Peromyscus maniculatus	17	0.170	20.5	0.219	Heusner (1991)
Rodentia	Muridae	Peromyscus maniculatus	18.02	0.203			Lovegrove (2000) White & Saumann (2002)
Rodentia	Muridae	Peromyscus maniculatus	18.95	0.220			Hart $(1971)$
Rodentia	Muridae	Peromyscus maniculatus	19	0.212			Hart (1971)
Rodentia	Muridae	Peromyscus maniculatus	19-1	0.217			Lovegrove (2003)
Rodentia	Muridae	Peromyscus maniculatus	19.53	0.222			White & Seymour (2003)
Rodentia	Muridae	Peromyscus maniculatus	20.38	0.209			White & Seymour (2003)
Rodentia	Muridae	Peromyscus maniculatus	22	0.245			Hart (1971)
Rodentia	Muridae	Peromyscus maniculatus	22.8	0.206			White & Seymour (2003)
Rodentia	Muridae	Peromyscus maniculatus	23.19	0.257			White & Seymour (2003)
Rodentia	Muridae	Peromyscus maniculatus	24.2	0.225			Lovegrove (2003)
Rodentia	Muridae	Peromyscus maniculatus	25	0.251	66.1	0.511	Hart (1971) Hart (1071)
Rodentia	Muridae	Peromyscus megalops Paromyscus magalops	00 66-2	0.515	00.1	0.311	Hart $(19/1)$ White & Seymour (2003)
Rodentia	Muridae	Peromyscus megatops Peromyscus oreas	24.58	0.243	24.6	0.243	White & Seymour (2003)
Rodentia	Muridae	Peromyscus polionotus	12	0.120	12.0	0.120	Lovegrove (2003)
Rodentia	Muridae	Peromyscus sitkensis	28.3	0.261	28.3	0.261	White & Seymour (2003)
Rodentia	Muridae	Peromyscus truei	33	0.256	33.1	0.307	Lovegrove (2000)
Rodentia	Muridae	Peromyscus truei	33	0.350			Hart (1971)
Rodentia	Muridae	Peromyscus truei	33.2	0.283			White & Seymour (2003)
Rodentia	Muridae	Peromyscus truei	33.3	0.349			White & Seymour (2003)
Rodentia	Muridae	Petromyscus collinus	20.41	0.115	20.4	0.115	Lovegrove (2003)
Rodentia	Muridae	Phenacomys intermedius	21.5	0.375	21.5	0.375	White & Seymour (2003)
Rodentia	Muridae	Phodopus sungorus	25.7	0.228	31.3	0.313	White & Seymour (2003)
Rodentia	Muridae	Phodopus sungorus	31.4	0.329			Lovegrove (2003)
Rodentia	Muridae	Phodopus sungorus	33.2	0.300			Heusner (1991)
Rodentia	Muridae	Phodopus sungorus Phyllotia damaini	35.9	0.425	47.0	0.222	Lovegrove (2000)
Rodentia	Muridae	Phyllotis darwini	49	0.367	470	0 555	White & Seymour (2003)
Rodentia	Muridae	Phyllotis darwini	59	0.398			White & Seymour (2003)
Rodentia	Muridae	Phyllotis magister	62.8	0.385	62.8	0.385	White & Seymour (2003)
Rodentia	Muridae	Phyllotis xanthopygus	55	0.316	55.0	0.316	White & Seymour (2003)
Rodentia	Muridae	Podomys floridanus	30.8	0.288	30.8	0.288	White & Seymour (2003)
Rodentia	Muridae	Pseudomys gracilicaudatus	79.8	0.467	79.8	0.467	White & Seymour (2003)
Rodentia	Muridae	Pseudomys hermannsburgensis	12.2	0.130	12.2	0.130	White & Seymour (2003)
Rodentia	Muridae	Rattus colletti	165.7	0.686	165.7	0.686	White & Seymour (2003)
Rodentia	Muridae	Rattus fuscipes	76	0.471	76.0	0.471	White & Seymour (2003)
Rodentia	Muridae	Rattus lutreolus	109	0.353	109.0	0.353	White & Seymour (2003)
Rodentia	Muridae	Rattus norvegicus	160	1.160	206.9	1.404	Hart (1971) Hart (1071)
Rodentia	Muridae	Rattus norvegicus	170	0.048			Hart (1971)
Rodentia	Muridae	Rattus norvegicus	170	0.960			Heusper $(1991)$
Rodentia	Muridae	Rattus norvegicus	225	1.506			Hart (1971)
Rodentia	Muridae	Rattus norvegicus	250	2.092			Hart (1971)
Rodentia	Muridae	Rattus norvegicus	390	2.393			Hart (1971)
Rodentia	Muridae	Rattus rattus	117	0.770	117.0	0.770	Heusner (1991)
Rodentia	Muridae	Rattus sordidus	187	0.595	187.0	0.595	White & Seymour (2003)
Rodentia	Muridae	Rattus villosissimus	185	0.585	215.3	0.690	Lovegrove (2003)
Rodentia	Muridae	Rattus villosissimus	250.6	0.813			White & Seymour (2003)
Rodentia	Muridae	Reithrodon auritus	78.7	0.428	78.7	0.428	Lovegrove (2003)
Rodentia	Muridae	Reithrodontomys megalotis	9	0.130	9.0	0.130	Heusner (1991)
Rodentia	Muridae	Rhabdomys pumilio	39°0 61.2	0.179	39·0 68.1	0.179	White & Seymour (2003)
Rodentia	Muridae	Saccostomus campestris	75.7	0.261	00.1	0.274	L ovegrove (2003)
Rodentia	Muridae	Scotinomys teguing	12	0.174	12.0	0.174	White & Seymour (2003)
Rodentia	Muridae	Scotinomys regaind Scotinomys xerampelinus	15.2	0.178	15.2	0.178	White & Seymour (2003)
Rodentia	Muridae	Sekeetamys calurus	56.9	0.248	63.6	0.274	White & Seymour (2003)
Rodentia	Muridae	Sekeetamys calurus	71.2	0.303			Lovegrove (2003)
Rodentia	Muridae	Sigmodon alleni	137.8	1.134	137.8	1.134	White & Seymour (2003)
Rodentia	Muridae	Sigmodon fulviventer	137.8	1.157	137.8	1.157	White & Seymour (2003)
Rodentia	Muridae	Sigmodon hispidus	139.3	1.285	159.6	1.085	White & Seymour (2003)
Rodentia	Muridae	Sigmodon hispidus	152.4	0.710			Heusner (1991)
Rodentia	Muridae	Sigmodon hispidus	191.6	1.400	100 6	1.040	Lovegrove (2003)
Rodentia	Muridae	Sigmodon leucotis	128.6	1.040	128.6	1.040	White & Seymour (2003)
Rodentia	Muridae	Sigmodon ochrognathus	115.1	0.105	115.1	0.105	White & Seymour (2003)
Rodentia	Muridae	Steelomys pratensis Stochomys longicaudatus	37.34 87.32	0.550	37.3	0.547	Winte & Seymour (2003) Heusper (1901)
Rodentia	Muridae	Stochomys longicaudatus	84.2	0.544	05 5	0 577	White & Sevmour (2003)
Rodentia	Muridae	Tachyoryctes splendens	171	0.811	197.0	0.856	Hart (1971)

Order	Family	Species	Mass (g)	BMR (W)	Species avg. mass (g)	Species avg. BMR (W)	References
Rodentia	Muridae	Tachyoryctes splendens	191	0.842			White & Seymour (2003)
Rodentia	Muridae	Tachyoryctes splendens	234	0.920			Heusner (1991)
Rodentia	Muridae	Tatera afra	106.5	1.016	106.5	1.016	White & Seymour (2003)
Rodentia	Muridae	Tatera indica Tatera in dia n	86.8	0.421	86.9	0.422	Lovegrove (2003)
Rodentia	Muridae	Tatera indica Tatera leucogaster	8/	0.422	145.2	0.752	L ovogrovo (2000)
Rodentia	Muridae	Tatera leucogaster	157.62	0.740	145.2	0 752	White & Seymour (2003)
Rodentia	Muridae	Thallomys nigricauda	124.7	0.382	124.7	0.382	Lovegrove (2000)
Rodentia	Muridae	Thallomys paedulcus	132.4	0.487	132.4	0.487	White & Seymour (2003)
Rodentia	Muridae	Uromys caudimaculatus	812	3.184	812.0	3.184	White & Seymour (2003)
Rodentia	Myoxidae	Graphiurus murinus	38.43	0.225	38.4	0.225	Lovegrove (2003)
Rodentia	Myoxidae	Graphiurus ocularis	67.8	0.370	67.8	0.370	White & Seymour (2003)
Rodentia	Myoxidae	Muscardinus avellanarius	23.5	0.351	23.5	0.351	White & Seymour (2003)
Rodentia	Myoxidae	Myoxus glis	152	0.500	174.4	0.664	Heusner (1991)
Rodentia	Myoxidae	Myoxus glis	200	0.881	112.0	0 (75	White & Seymour (2003)
Rodentia	Octodontidae	Aconaemys Juscus	112	0.675	112.0	0.675	White & Seymour (2003)
Rodentia	Octodontidae	Octodon degus	193	0.949	199.6	0.958	White & Seymour (2003)
Rodentia	Octodontidae	Octodon degus	206.4	0.966	177 0	0 950	Lovegrove (2000)
Rodentia	Octodontidae	Octodon lunatus	173.2	0.957	173.2	0.957	White & Seymour (2003)
Rodentia	Octodontidae	Octodontomys gliroides	152	0.729	154.1	0.715	White & Seymour (2003)
Rodentia	Octodontidae	Octodontomys gliroides	156.3	0.702			Lovegrove (2000)
Rodentia	Octodontidae	Octomys mimax	118.6	0.642	118.6	0.642	White & Seymour (2003)
Rodentia	Octodontidae	Spalacopus cyanus	109.5	0.520	126.2	0.561	Lovegrove (2000)
Rodentia	Octodontidae	Spalacopus cyanus	135	0.596			White & Seymour (2003)
Rodentia	Octodontidae	Spalacopus cyanus	136	0.570			Heusner (1991)
Rodentia	Octodontidae	Tympanoctomys barrerae	71.4	0.430	71.4	0.430	White & Seymour (2003)
Rodentia	Peditidae	Pedetes capensis	2 300	4.427	2 300.0	4.427	White & Seymour (2003)
Rodentia	Sciuridae	Ammospermophilus leucurus	/5.6	0.439	94.1	0.211	Lovegrove (2003) White & Sournour (2003)
Rodentia	Sciuridae	Ammospermophilus leucurus	95.7	0.540			Heusper (1991)
Rodentia	Sciuridae	Ammospermophilus leucurus	112.8	0.550			Heusner (1991)
Rodentia	Sciuridae	Cvnomvs ludovicianus	1 112.3	2.358	1 112.3	2.358	White & Seymour (2003)
Rodentia	Sciuridae	Epixerus wilsoni	460	1.347	460.0	1.347	White & Seymour (2003)
Rodentia	Sciuridae	Funisciurus anerythrus	63	0.580	63.0	0.580	Heusner (1991)
Rodentia	Sciuridae	Funisciurus congicus	112.3	0.533	112.3	0.533	White & Seymour (2003)
Rodentia	Sciuridae	Funisciurus isabella	60	0.570	60.0	0.570	White & Seymour (2003)
Rodentia	Sciuridae	Funisciurus lemniscatus	95	0.500	95.0	0.500	Heusner (1991)
Rodentia	Sciuridae	Funisciurus pyrrhopus	244	1.011	244.0	1.011	White & Seymour (2003)
Rodentia	Sciuridae	Glaucomys volans	62.8	0.370	67.4	0.414	Heusner (1991)
Rodentia	Sciuridae	Glaucomys volans	64·25	0.500			White & Seymour (2003)
Rodentia	Sciuridae	Heliosciurus rufobrachium	230	0.744	230.0	0.744	White & Seymour (2003)
Rodentia	Sciuridae	Marmota flaviventris	4 295	8.626	4 295.0	8.626	White & Seymour (2003)
Rodentia	Sciuridae	Marmota monax	2 650	3.696	2 650.0	3.696	White & Seymour (2003)
Rodentia	Sciuridae	Paraxerus cepapi	223.6	0.811	223.6	0.811	White & Seymour (2003)
Rodentia	Sciuridae	Paraxerus palliatus	206	0.977	274.8	1.191	White & Seymour (2003)
Rodentia	Sciuridae	Paraxerus palliatus	366.6	1.452			White & Seymour (2003)
Rodentia	Sciuridae	Sciurus aberti	624	2.402	624.0	2.402	White & Seymour (2003)
Rodentia	Sciuridae	Sciurus carolinensis	440	2.062	440.0	2.062	White & Seymour (2003)
Rodentia	Sciuridae	Spermophilus armatus	307	1.062	313.2	0.915	Lovegrove (2000)
Rodentia	Sciuridae	Spermophilus armatus	312.8	0.821			White & Sournour (2002)
Rodentia	Sciuridae	Spermophilus beechevi	599.6	1.773	599.6	1.773	White & Seymour (2003)
Rodentia	Sciuridae	Spermophilus beldingi	288.56	0.800	293.7	0.796	Heusner (1991)
Rodentia	Sciuridae	Spermophilus beldingi	289.8	0.889	_, , ,		Lovegrove (2000)
Rodentia	Sciuridae	Spermophilus beldingi	303	0.710			White & Seymour (2003)
Rodentia	Sciuridae	Spermophilus citellus	240	1.272	240.0	1.272	White & Seymour (2003)
Rodentia	Sciuridae	Spermophilus franklinii	607	2.190	607.0	2.190	Heusner (1991)
Rodentia	Sciuridae	Spermophilus lateralis	217.6	1.317	249.6	0.967	Lovegrove (2000)
Rodentia	Sciuridae	Spermophilus lateralis	237	0.800			White & Seymour (2003)
Rodentia	Sciuridae	Spermophilus lateralis	270.16	0.740			Heusner (1991)
Rodentia	Sciuridae	Spermophilus lateralis	278.7	1.119	240.0	0.(20)	Lovegrove (2003)
Rodentia	Sciuridae	Spermophilus monavensis	240	0.629	240.0	0.629	White & Seymour (2003)
Rodentia	Sciuridae	Spermophilus parryii Spermophilus viehardsonii	050	2.901	050·0 266.3	2.901	L evegreve (2000)
Rodentia	Sciuridae	Spermophilus richardsonii	273.07	0.740	200.3	0 / 00	Heusner (1991)
Rodentia	Sciuridae	Spermophilus richardsonii	274	0.734			White & Seymour (2003)
Rodentia	Sciuridae	Spermophilus saturatus	252.2	0.900	256.6	0.849	Lovegrove (2000)
Rodentia	Sciuridae	Spermophilus saturatus	261.15	0.800			Heusner (1991)
Rodentia	Sciuridae	Spermophilus spilosoma	157.8	0.500	170.4	0.543	Heusner (1991)
Rodentia	Sciuridae	Spermophilus spilosoma	174	0.514			White & Seymour (2003)
Rodentia	Sciuridae	Spermophilus spilosoma	180.3	0.624			Lovegrove (2000)

Order	Family	Species	Mass (g)	BMR (W)	Species avg. mass (g)	Species avg. BMR (W)	References
Rodentia	Sciuridae	Spermophilus tereticaudus	90.8	0.334	125.1	0.501	Lovegrove (2003)
Rodentia	Sciuridae	Spermophilus tereticaudus	129	0.720			Hart (1971)
Rodentia	Sciuridae	Spermophilus tereticaudus	167	0.522			White & Seymour (2003)
Rodentia	Sciuridae	Spermophilus townsendii	212.52	0.600	224.0	0.634	Heusner (1991)
Rodentia	Sciuridae	Spermophilus townsendii	229	0.587			White & Seymour (2003)
Rodentia	Sciuridae	Spermophilus townsendii	231	0.722			Lovegrove (2000)
Rodentia	Sciuridae	Spermophilus tridecemlineatus	182	0.579	198.4	0.983	Lovegrove (2000)
Rodentia	Sciuridae	Spermophilus tridecemlineatus	205.4	0.783			White & Seymour (2003)
Rodentia	Sciuridae	Spermophilus tridecemlineatus	209	2.099			Hart (1971)
Rodentia	Sciuridae	Spermophilus undulatus	500	2.789	698.0	3.601	Hart (1971)
Rodentia	Sciuridae	Spermophilus undulatus	680	3.721			White & Seymour (2003)
Rodentia	Sciuridae	Spermophilus undulatus	1 000	4.500			Heusner (1991)
Rodentia	Sciuridae	Tamias alpinus	39	0.322	39.0	0.322	White & Seymour (2003)
Rodentia	Sciuridae	Tamias amoenus	52.7	0.430	55.7	0.500	Heusner (1991)
Rodentia	Sciuridae	Tamias amoenus	57.1	0.537			White & Seymour (2003)
Rodentia	Sciuridae	Tamias amoenus	57.3	0.540			Lovegrove (2003)
Rodentia	Sciuridae	Tamias merriami	75	0.440	76.9	0.459	White & Seymour (2003)
Rodentia	Sciuridae	Tamias merriami	78.9	0.480			Heusner (1991)
Rodentia	Sciuridae	Tamias minimus	45.8	0.406	49.3	0.349	White & Seymour (2003)
Rodentia	Sciuridae	Tamias minimus	53	0.300			Heusner (1991)
Rodentia	Sciuridae	Tamias palmeri	69.4	0.631	69.4	0.631	White & Seymour (2003)
Rodentia	Sciuridae	Tamias striatus	87.4	0.502	89.6	0.813	White & Seymour (2003)
Rodentia	Sciuridae	Tamias striatus	91.8	1.316	0,0	0.015	Lovegrove (2000)
Rodentia	Sciuridae	Tamiasciurus hudsonicus	202	1.803	219.6	1.615	White & Seymour (2003)
Rodentia	Sciuridae	Tamiasciurus hudsonicus	224	1.410			Heusner (1991)
Rodentia	Sciuridae	Tamiasciurus hudsonicus	225	1.883			Hart (1971)
Rodentia	Sciuridae	Tamiasciurus hudsonicus	228-3	1.420			White & Seymour (2003)
Rodentia	Sciuridae	Xerus inquris	515.3	1.731	528.5	1.775	Lovegrove (2000)
Rodentia	Sciuridae	Xerus inauris	542	1.820	0200	1 1 1 0	White & Seymour (2003)
Rodentia	Sciuridae	Xerus princens	602	1.897	614.4	1.936	White & Seymour (2003)
Rodentia	Sciuridae	Xerus princeps	627	1.976	0111	1 950	Lovegrove (2000)
Scandentia	Tupajidae	Ptilocercus lowii	57.5	0.240	57.5	0.240	Heusner (1991)
Scandentia	Tupaiidae	Tunaia glis	123	0.522	123.0	0.522	White & Seymour (2003)
Scandentia	Tupaiidae	Urogale everetti	260.6	1.250	260.6	1.250	White & Seymour (2003)
Sirenia	Trichechidae	Trichechus inunguis	165 223	64.520	167 594.5	55.015	Lovegrove (2000)
Sirenia	Trichechidae	Trichechus inunguis	170 000	46.910	107 551 5	55 015	Heusner (1991)
Tubulidentata	Orveteropodidae	Orveteronus afer	48 000	34.275	48 000.0	34.275	White & Seymour (2003)
Xenarthra	Bradypodidae	Bradynus variegatus	3 790	3.827	3 790.0	3.827	White & Seymour (2003)
Xenarthra	Dasypodidae	Cabassous centralis	3 810	4.527	4 061.7	4.812	Lovegrove (2000)
Xenarthra	Dasypodidae	Cabassous centralis	4 330	5.116	1001 /	1012	White & Seymour (2003)
Xenarthra	Dasypodidae	Chaetophractus nationi	2 1 50	3.118	2 150.0	3.118	White & Seymour (2003)
Xenarthra	Dasypodidae	Chaetophractus vellerosus	1 110	1.707	1 110.0	1.707	White & Seymour (2003)
Xenarthra	Dasypodidae	Chaetophractus villosus	4 540	4.508	4 540.0	4.508	White & Seymour (2003)
Xenarthra	Dasypodidae	Dasvpus novemcinctus	3 320	4.490	3 413.7	4.655	Heusner (1991)
Xenarthra	Dasypodidae	Dasypus novemcinctus	3 510	4.825	5 115 /	1 000	White & Seymour (2003)
Xenarthra	Dasypodidae	Euphractus sexcinctus	8 190	6.901	8 190.0	6.901	White & Seymour (2003)
Xenarthra	Dasypodidae	Priodontes maximus	45 190	16.892	45 190.0	16.892	White & Seymour (2003)
Xenarthra	Dasypodidae	Tolvneutes matacus	1 160	1.172	1 160.0	1.172	White & Seymour (2003)
Xenarthra	Dasypodidae	Zaedvus nichiv	1 740	2.192	1 740.0	2.192	White & Seymour (2003)
Xenarthra	Megalonychidae	Cholognus hoffmanni	3 770	3.364	4 005.2	3.891	White & Seymour (2003)
Xenarthra	Megalonychidae	Cholognus hoffmanni	4 010	3.892	1005 2	5 0 1	Lovegrove (2000)
Xenarthra	Megalonychidae	Choloepus hoffmanni	4 250	4.500			Heusner (1991)
Xenarthra	Myrmeconhagidae	Cvelones didaetylus	- 250	0.636	240.0	0.636	White & Seymour (2003)
Xenarthra	Myrmeconhagidae	Myrmeconhaga tridactyla	30,600	14.543	30 600.0	14.543	White & Seymour (2003)
Xenarthra	Myrmeconhagidae	Tamandua mexicana	3 500	5.077	3 884.7	5.124	Lovegrove (2000)
Xenarthra	Myrmeconhagidae	Tamandua mexicana	3 077	5.52/	5 00+ 2	5 124	White & Seymour (2002)
Xenarthra	Myrmeconhagidae	Tamandua mexicana	4 210	4.700			Heusper (1001)
Xenarthra	Myrmeconhagidae	Tamandua tetradaetula	3 500	5.015	3 500.0	5.015	White & Seymour (2003)
	mjimeophagidae	sananana nenatutiytu	5 500	5 015	5 500 0	5 015	

© 2004 British Ecological Society, *Functional Ecology*, **18**, 257–282

0.389 075 625-1.198 070 7082.40.568 201 724-1.571 328 8363.70.661 431 752-1.172 116 0154.60.745 139 266-0.968 529 7645.6	0.063 0.027 0.067 0.108 0.103 0.102 0.131 0.122
0.568 201 724       -1.571 328 836       3.7         0.661 431 752       -1.172 116 015       4.6         0.745 139 266       -0.968 529 764       5.6	0.027 0.067 0.108 0.103 0.102 0.131 0.122
0.661 431 752     -1.172 116 015     4.6       0.745 139 266     -0.968 529 764     5.6	0.067 0.108 0.103 0.102 0.131 0.122
0.745 139 266 -0.968 529 764 5.6	0.108 0.103 0.102 0.131 0.122
	0·103 0·102 0·131 0·122
0.864 688 449 -0.985 843 9 7.3	0·102 0·131 0·122
0.947 565 356 -0.992 687 641 8-9	0·131 0·122
1·052 690 015 –0·884 366 833 11·3	0.122
1·148 732 343 -0·914 990 175 14·1	
1·243 318 579 -0·784 506 412 17·5	0.164
1·347 316 514 -0·651 955 766 22·2	0.223
1·454 764 674 –0·612 176 627 28·5	0.244
1.553 081 125 -0.568 248 466 35.7	0.270
1.656 886 834 -0.512 975 406 45.4	0.307
1.760 953 626 -0.436 201 138 57.7	0.366
1·844 213 326 -0·355 015 962 69·9	0.442
1.952 822 747 -0.278 952 613 89.7	0.526
2.055 702 395 -0.232 303 347 113.7	0.586
2:134 807 325 -0:146 755 532 136.4	0.713
2:253 844 347 -0:135 624 546 179.4	0.732
2:348 606 534 -0.029 454 704 223.2	0.934
2·439 805 622 -0·001 765 502 275·3	0.996
2:533 468 277 0:048 604 469 341.6	1.118
2:645 402 525 0:045 198 384 442:0	1.110
2.763 711 627 0.272 260 217 580.4	1.872
2.838 103 042 0.292 155 678 688.8	1.960
2.949 565 843 0.422 545 319 890.4	2.646
3.048 280 513 0.365 582 342 1 117.6	2.321
3.139 330 659 0.463 987 091 1 378.3	2.911
3:237 087 401 0:604 685 242 1 726:2	4.024
3:355 914 424 0:660 023 415 2 269.4	4.571
3·446 405 262 0·727 139 587 2 795·2	5.335
3.551 768 161 0.744 461 524 3 562.6	5.552
3.643 742 43 0.867 574 074 4 402.9	7.372
3.760 687 561 0.852 422 308 5 763.5	7.119
3.859 428 015 1.091 854 638 7 234.8	12.355
3·948 483 677 1·209 779 016 8 881·4	16.210
4·031 997 885 1·187 784 38 10 764·6	15.409
4.120 445 694 1.310 508 378 13 196.1	20.441
4:201 670 18 0:840 297 869 15 910:0	6.923
4·322 096 16 1·593 350 261 20 994·0	39.206
4·448 180 523 1·543 794 697 28 066·0	34.978
4·547 431 967 1·672 475 099 35 272·2	47.041
4.668 141 789 1.381 329 626 46 573.8	24.062
4.742 083 907 1.986 948 644 55 218.4	97.040
4·830 810 77 1·925 241 605 67 734·6	84.186
4.960 322 501       2.026 873 632       91 268.8       11	06.383
5·030 348 92 2·173 024 349 107 238·1 1·	48.944
5.149 112 499       2.162 811 081       140 965.4       1.	45.483
5·255 606 875 2·106 539 721 180 138·6 1	27.803
5.526 106 418 2.472 231 3 335 819.9 2	96.641
5·609 594 409 2·351 755 691 407 000·0 2	24.779
6.564 902 673       3.368 565 785       3 672 000.0       2 3	36.500