ALLOMETRIC STUDIES IN MAMMALIAN METABOLISM

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Allometric studies in mammalian metabolism

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Abstract

Terrestrial mammals span a size range of ~6 orders of magnitude from 2 g shrews to 4000 kg elephants. The consequences of these size differences are well known: the 4000 kg elephant lives longer than the 2 g shrew, for example, but the shrew's heart beats faster than the elephant's, and 1 g of shrew uses considerably more energy per unit time than 1 g of elephant. This thesis examines the effect of body mass (*M*) on a range of physiological variables and the nature of the residual variation about these relationships (i.e. variation not accounted for by body mass) both within and between species.

1. The relationship between mammalian basal metabolic rate (BMR) and body mass (*M*) has been the subject of regular investigation for over a century. The scaling exponent (b, where BMR = a M^{b}) remains a point of contention and arguments for and against geometric (b = 2/3) and quarter-power (b = 3/4) scaling continue to be made and rebutted in the literature. Here a new analysis of the allometry of mammalian BMR that accounts for variation associated with body temperature, digestive state and phylogeny finds no support for a metabolic scaling exponent of 3/4. Data encompassing five orders of magnitude variation in *M* and featuring 619 species from 19 mammalian orders show that BMR $\propto M^{2/3}$.

2. BMR is a useful measurement only if if the strictly defined conditions required for its measurement are adhered to. If variation associated with body temperature and digestive state is removed, the BMRs of eutherians and marsupials do not differ and no significant allometric exponent heterogeneity remains between orders. Of the 19 orders considered here, only Chiroptera and Dasyuromorphia have significantly different BMRs after eliminating body mass effects. The usefulness of BMR as a general measurement is supported by the observation that, after the removal of body mass effects, the residuals of BMR are significantly correlated with the residuals for a variety of physiological and ecological variables, including maximum metabolic rate, field metabolic rate, resting heart rate, litter size, and population density.

3. Mammalian BMR is one of the most widely measured physiological metrics, with the nature and causes of the interspecific relationship between *M* and BMR continuing to be investigated and debated. However, analysis of interspecific data both neglects considerable intraspecific variation and averages out the variation on which natural selection acts. This chapter assesses intraspecific variation in a range of physiological variables including BMR in the murid rodent, *Notomys alexis*. Most variables were significantly repeatable, suggesting that individual measurements were reliable. Mean values were similar to values predicted by allometry, but variation between individuals was considerable and in many cases approached 50% of that observed between species. A number of variables were significantly correlated, and the implications of these correlations are discussed.

4. The low BMR of fossorial mammals has been suggested either to compensate for the enormous energetic demands of subterranean foraging ("cost of burrowing hypothesis") or to prevent overheating in closed burrow systems ("thermal stress hypothesis"). These hypotheses are examined by comparing fossorial (subterranean foraging) and semi-fossorial (surface foraging) burrowing mammals. In support of the thermal stress hypothesis, the BMRs of mesic fossorial and semi-fossorial mammals can not be reliably distinguished, nor can the BMRs of large (> 77 g) arid fossorial and semi-fossorial

mammals. However, in support of the cost of burrowing hypothesis, small (< 77 g) arid fossorial species have significantly lower BMRs than semi-fossorial species of similar size. The greatly reduced BMR of small arid fossorial species may compensate for the enormous energetic demands of subterranean foraging in an environment where resources are sparse and widely distributed.

5. The allometric relationship between body mass and burrow cross-sectional area for burrowing animals holds across greater than six orders of magnitude variation in body mass. Only birds that construct relatively large burrows, and vermiform animals that construct relatively narrow burrows, are separated from the remaining burrowing species. No difference is found between the cross-sectional area of burrows constructed by fossorial and semi-fossorial mammals, although solitary fossorial mammals do construct significantly larger nest chambers than semi-fossorial and colonial fossorial mammals. These large nest chambers probably provide a better thermally insulated microenvironment and offset the thermoregulatory problems faced by these animals, which are characterised by low, labile body temperatures and poor thermoregulatory ability.

6. How many species covering what range of body masses are required to arrive at a reasonable estimate of the relationship between BMR and *M*? To answer this question, 4600 artificial species are generated based on the variation in BMR and *M* observed in extant mammals. Randomly selected subsets of the artificial species are examined to determine if calculation of a single 'true' allometric scaling exponent is currently possible. This analysis shows that 75 species spanning five orders of magnitude variation in body mass are sufficient to accurately determine the relationship between BMR and *M*.

7. Much of the interest in the relationship between BMR and *M* stems from the debate surrounding the value of the scaling exponent (b, where $\mathrm{BMR} \propto M^{b}$) with the relative merits of 2/3 and 3/4 exponents having now been debated for almost seven decades. Recent evidence suggests that phylogenetically informed (PI) comparative analyses are unable to resolve the debate because the value of the exponent depends on the evolutionary tree and the regression model used in the analysis. This chapter approaches the problem from a different perspective using randomly generated evolutionary trees and a homogenous selection of randomly generated 'artificial species' together with a literature compilation of PI and conventional scaling exponent estimates. It shows that although exponents estimated with PI and conventional regression methods can differ substantially, PI methods do not systematically bias exponent determination, suggesting that comparative analyses will remain a useful tool for resolving the debate.

8. Allometric data for different groups are most often compared using analysis of covariance (ANCOVA), a statistical procedure that compares treatment means (groups) after accounting for and removing their relationship with a covariate (often body mass). A requirement of ANCOVA is that the relationship with the covariate is uniform across groups, i.e. the regression slopes must be identical. This chapter describes a procedure (the Johnson-Neyman technique) that is applied following a finding of significantly heterogeneous regression slopes and allows for identification of the range of x-values at which there is a significant difference between groups. This allows potentially valuable information to be gleaned from data that might otherwise have been overlooked because of statistical limitations.

Acknowledgements

First and foremost, my friend, mentor and supervisor, Roger Seymour for providing a model of scientific endeavour to which to aspire, for always being accessible, for always being willing to discuss any topic of the moment, and for asking “why is the exponent ¾?” in a 3rd year tutorial. To Russ Baudinette for being accessible despite head of department/school responsibilities and for keeping me on track in Roger’s absence. To my family (Mum, Dad, Joel, Ben, Pat, Ellie, Sam, Seth, Faith, Nana, Sue, Peter and Paul) for always being supportive, despite not understanding why I would be interested in such things. To old friends (Mat, Brett, Cathy, Peter, and Jayme) for remaining. To new friends, particularly Kris, KJ, Ellen, Caroline, Graeme and Gege for reminding me that there is life within postgraduate study and for being there when I needed friends most. To Brett, Paul, and Phil, for creating a critical mass, bringing life and nerf balls to the lab, distracting me with honours theses, for quiet drinks in the bar, and for introducing me to the joys of Tuesday schnitters along with Brett, Maryka, and Tara. To Bec and Gail for noticing my absence during an extended illness. To Phil Withers, for our annual ANZSCPB discussions on phylogenetically informed methods and Frapps for always asking the same question. To my Maton ECW80C acoustic guitar for being both my greatest distraction and best relaxation. To Katie-Jane Orr and Phil Matthews, who somewhat foolishly agreed to proof read large swathes of this thesis. And finally, to life, for being so interesting.

Publications Arising

White C.R. and Seymour, R.S. (2003) Mammalian basal metabolic rate is proportional to body mass$^{2/3}$. *Proceedings of the National Academy of Sciences of the USA*. **100(7):4046-4049**

White, C.R. (2003) The influence of foraging mode and arid adaptation on the basal metabolic rates of burrowing mammals. *Physiological and Biochemical Zoology* **76(1):122-134**

White, C.R. (2003) Allometric analysis beyond heterogeneous regression slopes: Use of the Johnson-Neyman technique in comparative biology. *Physiological and Biochemical Zoology* **76(1):135-140**

White, C.R. and Seymour, R.S. (In Press) Does BMR contain a useful signal? Mammalian BMR allometry and correlations with a selection of physiological, ecological and life-history variables. *Physiological and Biochemical Zoology*

Introduction

> *"You can drop a mouse down a thousand-yard mine shaft; and, on arriving at the bottom, it gets a slight shock and walks away, provided that the ground is fairly soft. A rat is killed, a man is broken, a horse splashes"*
>
> 'On being the right size' J. B. S. Haldane (1928)

Size matters. Extant terrestrial mammals, the focus of this thesis, span ~6 orders of magnitude range in body mass from 2 g shrews to 4000 kg elephants. The effect of size is all pervasive, but it influences different variables in different ways: given that the volume (V, and therefore mass, M) of an object is proportional to the cube of some linear dimension ($M \propto l^3$), whilst its surface area (SA) is proportional to the square of a linear dimension ($\mathrm{SA} \propto l^2$) we can rearrange to find that

$$l \propto M^{1/3} \propto \mathrm{SA}^{1/2}$$

$$\therefore \mathrm{SA} \propto M^{2/3}$$

If you double an object's length, but keep its proportions the same, its surface therefore increases four-fold, its volume eight-fold. Surface area does not have an isometric relationship with mass, and this is true of a great many physiological variables (Huxley 1932; Gould 1966; Packard and Boardman 1987; 1988; 1999). Allometry (Greek: *allos*, other; *metron*, measure) is a technique used to describe this non-isometric variation by regressing a variable of interest against body mass, thereby describing the relationship. This relationship is often well described by a power equation of the form $y = a\,M^b$, where y is the variable of interest, a is the allometric coefficient, M is body mass and b is the allometric exponent. Allometric procedures are widely used throughout the biological sciences and have spawned a number of frequently cited books (McMahon and Bonner 1983; Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Brown and West 2000).

One of the most frequently investigated allometric relationships is that between M and basal metabolic rate (BMR). Given that heat produced through metabolic processes must be lost through the body surface, it can therefore be supposed that metabolic rate would also be proportional to $M^{2/3}$, so that the rate of heat production would be matched to the area of the surface over which it is dissipated. The idea that the effect of body size on metabolism might reflect simple geometric and physical processes was first supported by Max Rubner (1883), who found that, when corrected for differences in surface area, the metabolic rate of resting dogs was independent of mass. This finding, which came to be known as Rubner's surface law of metabolism, stood largely unchallenged for almost 50 years, until publication of Max

Kleiber's (1932) influential monograph. Kleiber (1932; 1961) found that metabolic rate was proportional to body mass raised to an exponent significantly greater than 2/3, and a value of 3/4 was subsequently adopted. Since that time, many biological variables have been linked with an allometric scaling exponent that is some multiple of 1/4 (see Brown and West 2000 for recent reviews) and several authors have attempted to explain the origin and theoretical derivation of these exponents (e.g. McMahon 1973; Economos 1982; Günther and Morgado 1982; Heusner 1982; Heusner 1991). 3/4 power scaling of mammalian BMR is a central paradigm of comparative physiology that has been accepted for over 70 years and remains in widespread use. Kleiber's (1932) monograph, for example, was cited in papers appearing in *Nature*, *Science* and *Proceedings of the National Academy of Sciences of the USA* throughout 2001, 2002 and 2003 (Gillooly *et al.* 2001; Niklas and Enquist 2001; Whitfield 2001; Darveau *et al.* 2002; 2002; Marquet 2002; Weibel 2002; West *et al.* 2002b; Cohen *et al.* 2003). Recently, attention has focused on theoretical explanations for quarter-power scaling based on the geometry of nutrient supply networks (West *et al.* 1997; Banavar *et al.* 1999; 2002b), four-dimensional biology (West *et al.* 1999) and an allometric cascade that links cellular and whole animal metabolism (Darveau *et al.* 2002; Hochachka *et al.* 2003). Proponents of these theories remain unable to reach a consensus on which is correct, and each group have presented arguments disputing competing theories (Banavar *et al.* 2002a; 2003; West *et al.* 2002a; 2003; Darveau *et al.* 2003). However, the debate over which theory accurately explains quarter-power scaling may be premature, because some authors maintain that there is insufficient evidence to adopt an exponent of 3/4 over 2/3 (e.g. Heusner 1991; Dodds *et al.* 2001). If progress toward understanding the non-isometric scaling of BMR is ever to be made it is first essential to know what the relationship actually is.

This thesis therefore focuses on the empirical side of the scaling exponent debate with reference to both interspecific and intraspecific variation. It addresses the value of the BMR scaling exponent (Chapters 1 and 2), correlated inter and intraspecific variation in BMR (Chapters 2, 3, and 4), and presents statistical and methodological requirements for accurate estimation of the scaling exponent and analysis of allometric data (Chapters 6, 7, and 8). Burrowing animals feature throughout the thesis, which also includes the first measurement of burrowing cost of transport for a semi-fossorial species (Chapter 3) and discusses the allometry of BMR and burrow geometry (Chapters 4 and 5), which are core components of the energy budgets of fossorial species.

1. Mammalian basal metabolic rate is proportional to body mass$^{2/3}$

Abstract

The relationship between mammalian basal metabolic rate (BMR, mL O_2 h^{-1}) and body mass (M, g) has been the subject of regular investigation for over a century. Typically, the relationship is expressed as an allometric equation of the form BMR = a M^{b}. The scaling exponent (b) is a point of contention throughout this body of literature, within which arguments for and against geometric (b = 2/3) and quarter-power (b = 3/4) scaling are made and rebutted. Recently, interest in the topic has been revived by published explanations for quarter-power scaling based on fractal nutrient supply networks and four-dimensional biology. Here a new analysis of the allometry of mammalian BMR that accounts for variation associated with body temperature, digestive state and phylogeny finds no support for a metabolic scaling exponent of 3/4. Data encompassing five orders of magnitude variation in M and featuring 619 species from 19 mammalian orders show that BMR $\propto M^{2/3}$.

Introduction

Pioneering work published by Max Rubner (1883) reported that mammalian BMR was proportional to $M^{2/3}$. In accordance with simple geometric and physical principles, it was therefore thought that an animal's rate of metabolic heat production was matched to the rate at which heat was dissipated through its body surface. However, Max Kleiber's (1932) influential monograph concluded that basal metabolic rate scaled not in proportion with surface area, but with an exponent significantly greater than that of Rubner's surface law. Kleiber's work was later supported by Brody's (1945) famous mouse-to-elephant curve, and an exponent of 3/4 (henceforth referred to as Kleiber's exponent) remains in widespread use. Quarter-power scaling is often regarded as ubiquitous in biology: metabolic rate has been reported as proportional to $M^{3/4}$ in organisms ranging from simple unicells to plants and endothermic vertebrates (Hemmingsen 1960; Gillooly *et al.* 2001). Kleiber's exponent has become so widely accepted that metabolic scaling relationships that deviate from an exponent of 3/4 are often considered somehow flawed or are summarily dismissed. However, examination of the species compositions of early studies (Kleiber 1932; Brody 1945) shows that they poorly reflect Mammalia. Most data points are derived from domestic species, which have been under artificial energetic constraints for many generations (Hayssen and Lacy 1985). Additionally, the order Artiodactyla is consistently over-represented; both

Kleiber's (1932) and Brody's (1945) data sets include ~20% artiodactyls, but only ~5% of Recent mammals are artiodactyls (Nowak 1999). Being near the upper mass limit of the regressions, these animals exert a disproportionate influence on the scaling exponent. Their inclusion is problematic, because microbial fermentation of cellulose may delay or prohibit entrance into a postabsorptive state (McNab 1997). This elevates metabolic rate above basal levels and, when coupled with a large body mass, artificially inflates the calculated scaling exponent. Examination of Brody's (1945) data reveals the same problems (Hayssen and Lacy 1985). Because measurement of BMR must be obtained from inactive, postabsorptive, adult, nonreproductive and thermoregulating animals in their inactive circadian phase and in a thermoneutral environment (McNab 1997), measurements for large herbivores must be excluded from analyses of mammalian BMR, or included with caution.

The problematic inclusion of ruminants was also recognised by Kleiber (1932), whose compilation included 13 data points derived from eight species (two steers, cow, man, woman, sheep, male dog, female dog, hen, pigeon, male rat, female rat, and ring dove). Kleiber addressed the problem by providing b values calculated for all 13 data points and for a subset of nine data points with ruminants excluded. Using Kleiber's (1932) data, exponents of 0.737 ($r^2 = 0.999$) and 0.727 ($r^2 = 0.999$) can be calculated for these groups, respectively. In this case quarter-power scaling remained following the exclusion of ruminants, because of the influence of the four data points for male and female dogs and humans. The large b value can then be attributed to the high metabolic rate of domestic carnivores (Hayssen and Lacy 1985; Elgar and Harvey 1987; McNab 1988a), and humans (180 – 200% of that predicted by the equations described below). Calculation of b from the remaining five data points yields a value of 0.667 ($r^2 = 0.999$). The widespread use and acceptance of Kleiber's exponent can probably be attributed to a remarkably tight regression fit (r^2). For Kleiber's thirteen data points, M alone explains 99.9% of the variation in BMR. To put this r^2 in perspective, 250,000 groups of 13 species were randomly selected from a list of 391 species compiled by Heusner (1991) (This compilation was selected because it includes data for domestic ruminants, as did Kleiber's). Each group had a mass range of 3 – 4 orders of magnitude to match Kleiber's data, which spanned 3.7 orders of magnitude. Of the 250,000 least square regressions, only four had an r^2 greater than 0.998 and none had an r^2 greater than 0.999. The strength of Kleiber's exponent therefore seems to stem from an exceedingly fortuitous selection of data.

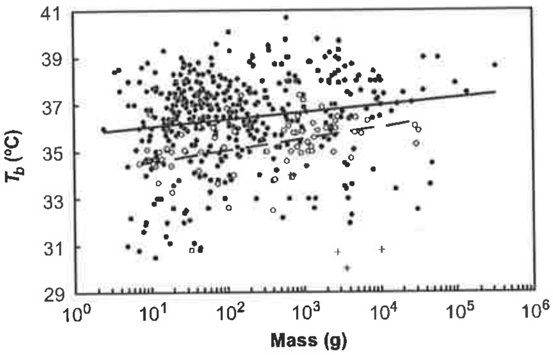

Figure 1.1. Relationship between body mass (M, g) and body temperature (T_b, °C) for eutherians (● and unbroken line: $T_b = 35.8 + 0.30 \log M$, n = 437), marsupials (○ and broken line: $T_b = 34.1 + 0.49 \log M$, n = 67) and monotremes (+, n = 4).

Another problem with previous analyses is that all neglect differences in body temperature (T_b, °C) between species. This is important because T_b and M are primary determinants of metabolic rate (Gillooly *et al.* 2001) and T_b is significantly correlated with M for marsupials (Withers *et al.* 2000) ($T_b = 34.1 + 0.49 \log M$, n = 66, Figure 1.1), eutherians (ANOVA $F_{1,436} = 21.5$, p = 0.01, $T_b = 35.8 + 0.30 \log M$, n = 437 , Figure 1.1) and mammals in general (ANOVA $F_{1,507} = 37.0$, $p < 0.001$, $T_b = 35.8 + 0.21 \log M$, n = 507). An accurate estimation of the relationship between BMR and M is therefore best obtained by normalising the measured BMRs of all species to a common T_b.

In the 70 years since Kleiber's monograph, a wealth of BMR and T_b data has accumulated. This report draws on the most comprehensive and representative database available, to analyse the relationship between BMR and body size. Although BMR is an artificial physiological construct that animals rarely show under natural conditions, it remains an established benchmark for comparing metabolic intensity between species. More importantly, if theoretical analyses are ever to explain the non-linear relationship between metabolic rate and body size, it is essential to establish what that relationship actually is, without confounding influences of T_b and digestive state.

Methods

Data for 619 species were compiled from the literature (Appendix A). Wherever possible, M, T_b and BMR were sourced from the same paper. Where multiple values were available for a species, the arithmetic mean was calculated. BMR and T_b values were accepted only if the animals were resting, normothermic, postabsorptive, inactive and conscious. Data that did not fulfil these criteria were disregarded. Adult body mass was obtained from multiple published sources when body mass was not provided in papers from which measurements were taken. The data were disregarded if no body mass could be found in the established literature. To allow for the overestimation of degrees of freedom problem inherent in comparative analyses of species data, a nested ANOVA was used to determine the appropriate taxonomic level at which averages should be calculated (Harvey and Pagel 1991). Nested ANOVA showed that order values capture 85% of the variation in M and 86% of the variation in BMR, and was therefore the appropriate level for analysis (Elgar and Harvey 1987). Data were log-transformed and genera values were calculated as the average of species within genera, family values were calculated as averages of genera within families and order values were calculated as the average of families within orders.

Least-square linear regressions of the form log(BMR) = log(a) + b log(M) were fitted to log-log transformed data. This enabled calculation of an allometric equation of the form BMR = a M^{b}. When T_b was available for a species (n = 507), BMR data were normalised to a T_b equal to the mean T_b of all species (36.2 °C). Order values were transformed using the average T_b of species within the order, using the same nested average calculation as used for BMR and M. Traditionally, correction for temperature differences is undertaken using Q_{10} principles (Guppy and Withers 1999; Gillooly *et al.* 2001) such that

$$\mathrm{BMR_c} = \mathrm{BMR} \cdot 10^{(T_c - T_b)\log(Q_{10})/10}$$

where BMR$_c$ is temperature corrected BMR, T_c is the temperature to which all observations are corrected (36.2 °C) and Q_{10} is the factorial increase in BMR associated with a temperature increase of 10 °C. To select the appropriate Q_{10} for temperature correction in this analysis, results obtained with a series of values between 2 and 4 were compared. A Q_{10} of 3.0 was used because this value produced the highest r^2 when log BMR$_c$ was regressed against log M, and therefore minimised the variation in BMR$_c$. As an alternative to Q_{10} principles, Gillooly *et al.* (2001) proposed a correction factor based on the “universal temperature dependence” (UTD) of biological processes, suggesting that correction using a single temperature-independent Q_{10} value could introduce an error as great as 15% over the range of biologically relevant temperatures (approx. 0 – 40 °C). UTD correction considers metabolic rate to be the sum of many biological reactions, where each reaction rate is proportional to the product of the concentration of reactants, the fluxes of reactants and the kinetic energy of the system. Although the potential error introduced by Q_{10} correction is likely to be considerably less than 15% within the modest T_b range in the present analysis (~30 – 40 °C), both Q_{10} and UTD correction methods were used. Only the results obtained with Q_{10} correction are presented, however, because UTD correction accounted for marginally less of the residual variation and did not alter the conclusions. No attempt was made to distinguish between BMR values obtained in the active (α) or resting (ρ) phase of the day. This did not compromise the study, because the ~33% elevation in BMR observed in the α phase (Kenagy and Vleck 1982) can be wholly accounted for with a Q_{10} of 3.0 and only a 2.4 °C difference between α and ρ T_b, which is within the range of observed mammalian daily T_b variation (Aschoff 1982). Assuming that BMR and T_b were measured in the same circadian phase, correction to a common T_b therefore accounts for circadian fluctuations in BMR.

A conservative approach was then adopted where lineages for which the conditions required for BMR measurement were suspected to be difficult or impossible to achieve were excluded. The lineages excluded were Artiodactyla, Macropodidae (Diprotodontia), Lagomorpha, and Soricidae (Insectivora). Exclusion of artiodactyls was considered necessary because the length of time for which they were fasted (2 – 3 days) was probably insufficient to produce a postabsorptive state (which requires 2 – 7 days to achieve in domestic ruminants (Blaxter 1962), but may be in fact unachievable (McNab 1997)). Similarly, macropod marsupials are large herbivores with a complex voluminous stomach that is a major site for microbial fermentation (Stevens and Hume 1995). Lagomorphs were excluded because their hindgut is a major site for microbial fermentation (Stevens and Hume 1995) and they have high metabolic rates relative to other eutherians (Hayssen and Lacy 1985), possibly associated with microbial fermentation. Shrews (Soricidae) were excluded because they may become hyperactive when postabsorptive, hence postabsorptive and inactive conditions are mutually exclusive (Speakman *et al.* 1993). Although some other lineages (e.g. Cetacea, Proboscidae) are not present in the data set, their absence stems solely from a lack of measurements that satisfy the basic requirements for BMR.

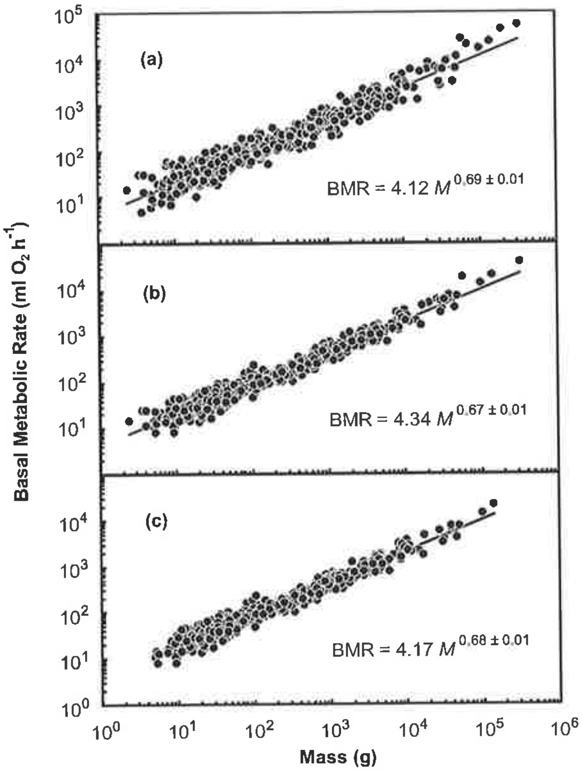

Figure 1.2. Relationship between mammalian body mass (*M*, g) and basal metabolic rate (BMR, mL O_2 h^{-1}) for (a) all data ($n = 619$, $r^2 = 0.94$), (b) data corrected to a common body temperature (36.2 °C) using a Q_{10} of 3.0 ($n = 507$, $r^2 = 0.96$) and (c) data corrected to 36.2 °C for all species excluding Artiodactyla, Lagomorpha, Soricidae (Insectivora), and Macropodidae (Diprotodontia) ($n = 469$, $r^2 = 0.96$). Exponents are shown with 95% confidence intervals.

Results

Both interspecific and interordinal analyses were made. For the 619 species for which BMR data have been published (Appendix A), *M* alone accounted for 94% of the interspecific variation in BMR, but the 95% confidence intervals of the allometric exponent (0.69) do not include 3/4 or 2/3 (Figure 1.2a). However, this finding may be misleading, because species values do not represent statistically independent data on which to base a comparison (Harvey and Pagel 1991). This leads to overestimation of degrees of freedom, which artificially narrows confidence intervals and can result in the false rejection of null hypotheses. The use of an average value calculated for some higher taxonomic level reduces degrees of freedom and addresses the non-independence problem inherent in non-phylogenetically informed

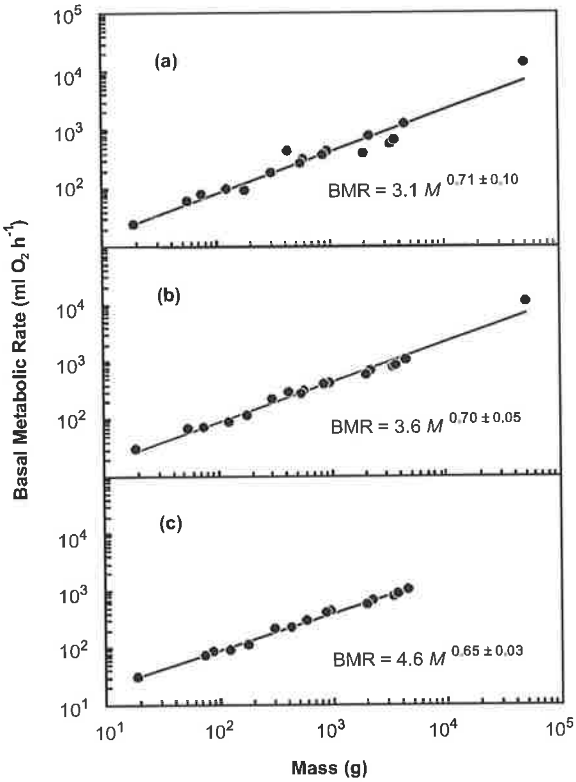

Figure 1.3. Relationship between body mass (M, g) and basal metabolic rate (BMR, mL O_2 h^{-1}) for mammalian orders (see methods for details) for (a) all data ($n = 17$, $r^2 = 0.94$), (b) data corrected to a common body temperature (36.2 °C) using a Q_{10} of 3.0 ($n = 17$, $r^2 = 0.98$) and (c) data corrected to 36.2 °C for all species excluding Artiodactyla, Lagomorpha, Soricidae (Insectivora), and Macropodidae (Diprotodontia) ($n = 15$, $r^2 = 0.99$). Exponents are shown with 95% confidence intervals.

analyses (Harvey and Pagel 1991). As has been previously demonstrated (Elgar and Harvey 1987), the order level was identified as that which captures a large proportion of the variation in M and BMR, but does not unnecessarily reduce sample size (see methods). For the 17 mammalian orders represented by at least three species, M also accounts for 94% of the variation in BMR, but the allometric exponent is not significantly different from 3/4 or 2/3 (Figure 1.3a). Additionally, the variation not accounted for by M (the BMR residuals) is significantly positively correlated with T_b for both the interspecific (BMR residual = $0.05\ T_b - 1.8$; $n = 507$, $r^2 = 0.32$, $p < 0.001$) and interordinal (BMR residual = $0.07\ T_b - 2.4$; $n = 17$, $r^2 = 0.76$, $p < 0.001$) analyses. When BMR values are normalised to a T_b of 36.2 °C using Q_{10} principles, both the interspecific and interordinal allometric exponents decreased and neither was found to be significantly different from 2/3, while only the interspecific exponent was significantly different from 3/4 (Figures 1.2b and 1.3b). Finally, exclusion of Artiodactyla, Macropodidae (Diprotodontia), Lagomorpha, and Soricidae (Insectivora) further refined the predictions such that M and T_b accounted for 96% of the interspecific variation in BMR and 99% of the interordinal variation in BMR (Figures 1.2c and 1.3c). Both interspecific (0.68) and interordinal (0.65) allometric exponents were significantly different from 3/4 and were not significantly different from 2/3 (Figures 1.2c and 1.3c).

Discussion

This study finds that the BMR of mammals is proportional to $M^{2/3}$, as is the case for birds (Bennett and Harvey 1987; Reynolds and Lee 1996; Tieleman and Williams 2000; Frappell *et al.* 2001). The relationships presented here fail to account for only 4 % of the interspecific and 1% of the interordinal variation in mammalian BMR. Many factors have been suggested as proximal causes for the residual differences in mammalian BMR and investigation of these factors is likely to continue to be a fruitful area of investigation in the future. Factors that have been implicated so far include phylogeny (Hayssen and Lacy 1985; Elgar and Harvey 1987), diet (McNab 1988a), geography (Lovegrove 2000), aridity (Lovegrove 2000), habitat productivity (Lovegrove 2000; Mueller and Diamond 2001), and relative organ masses (Konarzewski and Diamond 1995). In many cases, separation of these influences is difficult, particularly when they are correlated or confounded (e.g. Cruz-Neto *et al.* 2001).

In addition to the statistical analyses presented here, the validity of a BMR scaling exponent of 2/3 can be investigated by using this relationship to predict allometric exponents for complimentary variables (e.g. home range) that can reasonably be thought to be related to BMR. Such comparisons have previously been approached from the invalid assumption that BMR is proportional to $M^{3/4}$. For example, a recent analysis of home range scaling (Haskell *et al.* 2002) used a BMR exponent of 0.75 and predicted home range scaling exponents of 0.83, 1.33 and 1.5 for terrestrial mammalian herbivores, terrestrial mammalian carnivores, and terrestrial avian carnivores, respectively (Haskell *et al.* 2002). These predictions differed from the observed exponents (0.83, 1.21 and 1.37) by an average of 0.09. Recalculation of the predicted home range scaling exponents using a BMR scaling exponent of 0.67 yields predictions of 0.75, 1.25 and 1.42, which differ from the observed exponents by only 0.002. This strengthens the case for a 2/3 exponent by linking BMR with home range size, a variable that integrates behaviour, physiology and population density (Haskell *et al.* 2002).

The finding that BMR is proportional to $M^{2/3}$ challenges a 70-year-old paradigm and suggests that a common cause underlies the influence of M on BMR for endothermic homeotherms. An exponent of 2/3 questions recent explanations for quarter-power scaling (West *et al.* 1997; 1999; Banavar *et al.* 2002b; Darveau *et al.* 2002), and indicates that other explanations need to be sought. As the present analysis is concerned only with a description of the allometric relationship between BMR and M, any speculation regarding what factors might account for it has been avoided.

2. Does BMR contain a useful signal? Mammalian BMR allometry and correlations with a selection of physiological, ecological and life-history variables

Abstract

Basal metabolic rate (BMR, mL O_2 h^{-1}) is a useful measurement only if standard conditions are realised. This chapter features an analysis of the relationship between mammalian body mass (M, g) and BMR that accounts for variation associated with body temperature, digestive state and phylogeny. In contrast to the established paradigm that BMR $\propto M^{3/4}$, data from 619 species, representing 19 mammalian orders and encompassing five orders of magnitude variation in M, show that BMR $\propto M^{2/3}$. If variation associated with body temperature and digestive state are removed, the BMRs of eutherians, marsupials and birds do not differ and no significant allometric exponent heterogeneity remains between orders. The usefulness of BMR as a general measurement is supported by the observation that, after the removal of body mass effects, the residuals of BMR are significantly correlated with the residuals for a variety of physiological and ecological variables, including maximum metabolic rate, field metabolic rate, resting heart rate, lifespan, litter size, and population density.

Introduction

Most of the controversy surrounding the relationship between mammalian basal metabolic rate (BMR) and body mass (M, g) focuses on the value of the scaling exponent in the allometric equation, BMR = a M^b. Empirical support for a 3/4 exponent is based on species that poorly represent Mammalia and do not unequivocally reject an exponent of 2/3 (Dodds *et al.* 2001). Most analyses are compromised by inclusion of gut-fermenting species in which basal conditions are unlikely during measurement and neglect interspecific differences in body temperature (T_b, °C). Incorporation of T_b is important, because it is a primary determinant of metabolic rate (Gillooly *et al.* 2001) and it increases significantly with M for marsupials, eutherians and mammals in general (Chapter 1). An accurate estimation of the relationship between BMR and M is therefore best obtained by normalising the measured BMRs of all species to a common T_b and eliminating data from suspected non-postabsorptive animals.

Chapter 1 discusses the most comprehensive and representative database so far available for mammals. The analysis presented there accounts for variation associated with T_b

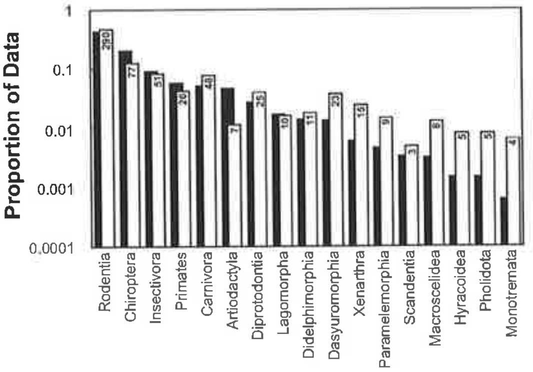

Figure 2.1. Comparison of contribution of mammalian orders to the present data set (unfilled bars, numbers represent sample size) and Mammalia as a whole (filled bars, data from (Nowak 1999)). Notoryctemorphia and Tubulidentata not shown: each includes a single species in the present analysis.

and digestive state in an allometric analysis of BMR and shows that BMR scales with body mass to the 0.68 ± 0.01 (95% CI) and that this conclusion is not affected by phylogeny. In this chapter, this data set is further examined to demonstrate the utility of BMR in relation to other physiological, ecological and life-history variables. Additionally, because the BMRs of birds are also proportional to $M^{2/3}$ (Bennett and Harvey 1987; Reynolds and Lee 1996; Tieleman and Williams 2000; Frappell *et al.* 2001), but birds have higher T_bs and BMRs than mammals (McNab 1966a; Calder 1984), a preliminary analysis of the effect of T_b on BMR across mammals and birds is made. This analysis tests the hypothesis that BMR differences between the two major radiations of endothermic homeotherms can be accounted for solely by T_b variation.

Methods

Allometry of mammalian BMR

Body mass (M, g), body temperature (T_b, °C) and basal metabolic rate (BMR, mL O_2 h^{-1}) data for 619 species representing 19 mammalian orders and encompassing five orders of magnitude variation in M were compiled from the literature (Figure 2.1, Appendix A). Data were selected according to strictly established guidelines (McNab 1997) and were included only if obtained when animals were inactive, postabsorptive, adult, non-reproductive and thermoregulating in a thermoneutral environment. No attempt was made to exclude

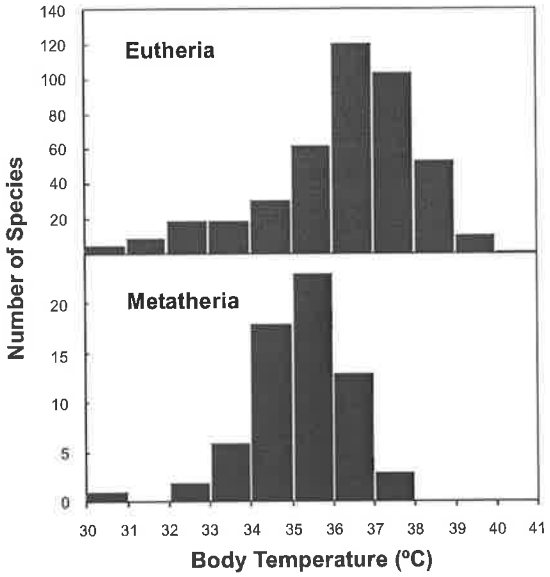

Figure 2.2. Body temperature (T_b, °C) distributions for eutherians (top) and metatherians (bottom). Mean (± s.d.) mammal T_b is 36.2 ± 1.9 °C (n = 507), eutherian T_b is 36.4 ± 1.8 °C (n = 437), metatherian T_b is 35.3 ± 1.2 °C (n = 66) and monotreme T_b is 31.4 ± 1.8 °C (n = 4).

measurements obtained during the active circadian phase. This did not compromise the study, however, because the elevated BMR observed in the active circadian phase (Kenagy and Vleck 1982) coincides with elevated body temperature (Aschoff 1982). Therefore, normalisation of BMR measurements to the mean T_b of species for which measurements are available (36.2 °C, n = 507, Figure 2.2) with the van't Hoff (Q_{10}) principle wholly accounts for circadian variation in BMR, providing that BMR and T_b were measured in the same circadian phase. Least square regressions of the form $\log(\mathrm{BMR}) = \log(\mathrm{a}) + \mathrm{b}\log(M)$ were fitted to log-log transformed data for both the unmodified and Q_{10}-normalised data. Additionally, a hierarchically nested ANOVA (Harvey and Pagel 1991) was used to determine the appropriate taxonomic level at which averages should be calculated to account for the problem of overestimation of degrees of freedom that is inherent in comparative analyses of species data. The order level was found to capture 85% of the variation in M and 86% of the variation in BMR, indicating that this was the appropriate level for analysis, in accordance with previous work (Elgar and Harvey 1987). BMR values for each order were normalised to the mean T_b using the hierarchically nested average T_b of species within the order.

The analysis was then repeated following exclusion of lineages for which BMR measurements were suspected to be unachievable. Artiodactyls were excluded because microbial fermentation of cellulose may delay or prohibit entrance into a postabsorptive state (McNab 1997); macropods and lagomorphs were excluded for the same reason. Shrews (Soricidae) were excluded because postabsorptive and inactive conditions may be mutually exclusive (Speakman *et al.* 1993). The absence of some other lineages (e.g. Cetacea, Proboscidae) stems solely from a lack of published BMR measurements. Data selected according to these criteria are henceforth referred to as 'conservative BMR', if no Q_{10}-normalisation was undertaken, or 'conservative Q_{10}-normalised BMR' if it was.

Interspecific allometries were also calculated for each of the orders for which data for more than three species spanning a body mass range greater than an order of magnitude were available, and for species from each of the six zoogeographic regions considered by Lovegrove (2000).

Variation in mammalian BMR

BMR variation was examined at the level of order and infraclass (monotremes were excluded from the infraclass comparison due to small sample size (n = 4) relative to eutherians (n = 546) and marsupials (n = 69). Allometric exponent heterogeneity was identified using ANOVA (order × log(M) interaction). The effect of order on BMR was then identified using ANCOVA, and pairs of significantly different orders were identified using BMR residuals (= log(measured BMR) - log(predicted BMR)) and the Tukey-Kramer H.S.D. test. Allometric exponent heterogeneity between infraclasses was examined using ANOVA (infraclass × log(M) interaction) and BMR differences between Eutheria and Metatheria were examined using ANCOVA. α was set at 0.05 for all comparisons.

Correlations between BMR and other physiological, ecological and life-history variables

Because many biological variables are potentially correlated due only to correlations with body mass (e.g. large animals tend to have both high BMRs and large home ranges), BMR residuals were compared with mass-independent residuals for a variety of variables (body surface area, field metabolic rate (FMR), maximum aerobic metabolic rate (MMR), resting heart rate, fecundity (young per year), litter size, number of litters produced per year, maximum recorded lifespan and population density). Data for these variables were obtained

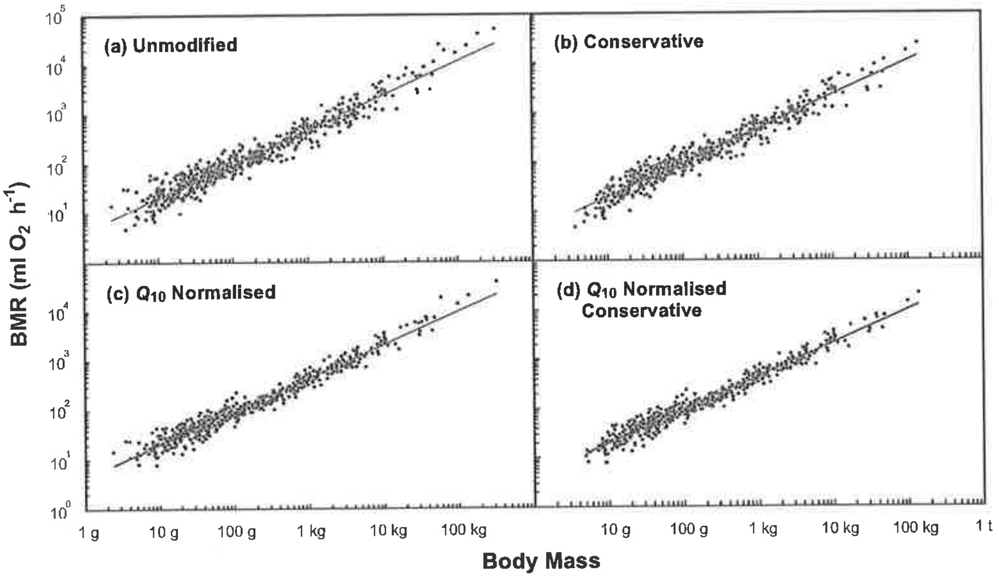

Figure 2.3. Interspecific relationships between mammalian body mass (*M*, g) and BMR for (a) all data (n = 619), (b) conservative data (n = 571, see methods for selection criteria), (c) all data normalised to a common body temperature of 36.2 °C (n = 507) and (d) conservative data normalised to a common body temperature of 36.2 °C (n = 469). Equations of the regression lines: (a) $\mathrm{BMR} = 4.12\,M^{0.687*}$, $r^2 = 0.94$; (b) $\mathrm{BMR} = 3.98\,M^{0.686*}$, $r^2 = 0.94$; (c) $\mathrm{BMR} = 4.34\,M^{0.672}$, $r^2 = 0.96$; (d) $\mathrm{BMR} = 4.17\,M^{0.675}$, $r^2 = 0.96$ (* denotes exponents that are significantly different from 2/3 [$p < 0.05$]).

from a combination of published allometric analyses and non-allometric studies (sources are provided with Table 2.4). Wherever possible, the allometric equation used to generate the residuals for the non-BMR variables was the published equation, but in some cases the equation and residuals were calculated from raw data. Comparisons were made both within Mammalia as a group, and within those orders for which sufficient data were available.

Results

Allometry of mammalian BMR

Body mass alone accounts for 94% of the interspecific variation in BMR, but the allometric exponent (0.687) is significantly different from both 2/3 and 3/4 (Figure 2.3a, Table 2.1). However, this finding potentially represents a Type I error, because species-values are often not statistically independent, which leads to overestimated degrees of freedom and erroneously narrowed confidence intervals (Harvey and Pagel 1991). This problem is

Table 2.1. Allometric parameters relating mammalian body mass (M, g) and basal metabolic rate (BMR, mL O_2 h^{-1}) according to the equation BMR = a M^b.

	n	a	b	r^2
Interspecific allometry				
Unmodified	619	4.12 (3.82-4.44)	0.687 ± 0.007 (0.674-0.701)	0.94
Conservative	571	3.98 (3.69-4.29)	0.686 ± 0.007 (0.672-0.700)	0.94
Q_{10}-normalised	507	4.34 (4.06-4.63)	0.672 ± 0.006 (0.660-0.684)	0.96
Conservative Q_{10}-normalised	469	4.17 (3.89-4.47)	0.675 ± 0.006 (0.662-0.687)	0.96
Interordinal allometry				
Unmodified	17	3.11 (1.6-6.04)	0.71 ± 0.05 (0.61-0.80)	0.94
Conservative	15	4.35 (2.57-7.35)	0.64 ± 0.04 (0.56-0.72)	0.96
Q_{10}-normalised	17	3.57 (2.51-5.07)	0.70 ± 0.02 (0.66-0.75)	0.98
Conservative Q_{10}-normalised	15	4.58 (3.70-5.66)	0.65 ± 0.01 (0.62-0.68)	0.99

Note to Table 2.1: Data are presented ± SE. Values in parentheses are 95% confidence limits. Regressions were calculated with the following combinations of species - (unmodified) all data (n = 619), (conservative) data with BMRs for Artiodactyla, Soricidae (Insectivora), Macropodidae (Diprotodontia) and Lagomorpha excluded (n = 571), (Q_{10} normalised) all data normalised to a common body temperature of 36.2 °C (n = 507) according to Q_{10} principles with a Q_{10} of 3.0 and (conservative Q_{10} normalised) data normalised to a common body temperature of 36.2 °C with BMRs for Artiodactyla, Soricidae (Insectivora), Macropodidae (Diprotodontia) and Lagomorpha excluded (n = 469).

overcome by using average values calculated for each of the 17 orders represented by at least three species. Interestingly, M also accounts for 94% of the interordinal variation in mammalian BMR, but the confidence interval includes both 2/3 and 3/4 (Table 2.1). T_b is significantly correlated with BMR residuals in both the interspecific analysis ($r = 0.57$, $n = 507$, $p < 0.001$) and the interordinal analysis ($r = 0.87$, $n = 17$, $p < 0.001$) (Figure 2.4). Normalisation of BMR measurements to a common T_b of 36.2 °C ($Q_{10} = 3.0$, Chapter 1) decreases both the interspecific and interordinal BMR scaling exponents: neither is significantly different from 2/3, while only the interspecific exponent is significantly different

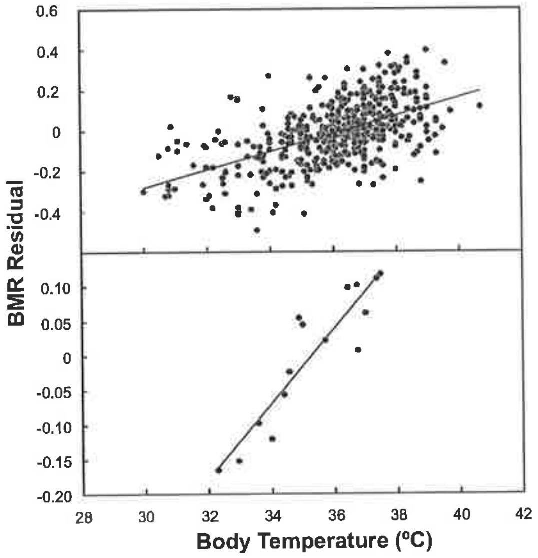

Figure 2.4. Relationship between body temperature and residual variation in conservative BMR (see methods) for species (top) and order (bottom) data. Both correlations are significant ($p < 0.05$).

from 3/4 (Figure 2.2c, Table 2.1). Exclusion of suspected non-basal measurements (Artiodactyla, Macropodidae, Lagomorpha and Soricidae) also refined the predictions such that both the interspecific and interordinal exponents are significantly different from 3/4, although the interspecific exponent remains significantly different from 2/3 (Figure 2.3c, Table 2.1). When data are normalised to 36.2 °C and suspected non-basal measurements excluded, however, both the interspecific (0.675) and interordinal (0.65) allometric exponents are significantly different from 3/4 but not significantly different from 2/3 (Figures 2.3d and 2.5, Table 2.1).

Variation in BMR between mammalian taxa and zoogeographic regions

Body mass accounts for 96% of the interspecific variation and 99% of the interordinal variation in Q_{10}-normalised BMR, following exclusion of likely non-basal measurements (Table 2.1). At a given body mass, however, variation about the regression line remains considerable (Figure 2.6, Table 2.2). Despite the reduction in variation associated with Q_{10}-normalisation, the 'bowtie' pattern of residual variation remains (Lovegrove 2000). Maximum BMR variation occurs at the smallest and largest masses, whilst minimum

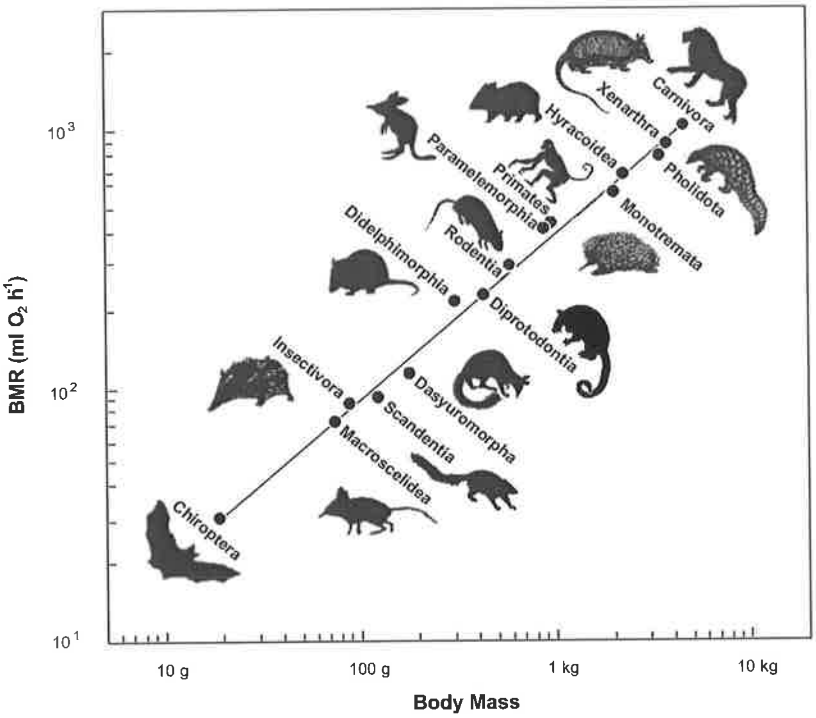

Figure 2.5. Relationship between body mass (M, g) and Q_{10}-normalised BMR (see methods) for orders represented by at least three species. BMR = 4.58 $M^{0.65}$, $r^2 = 0.99$.

variation occurs at an intermediate mass, the 'constrained body mass' (CBM = 350 g) of Lovegrove (2000) (Figure 2.7). Regression exponents for each of the 14 orders represented by at least three species are significantly heterogeneous between orders for unmodified data (ANOVA $F_{16,583} = 6.0$, $p < 0.0001$), but exponents from conservative Q_{10}-normalised data are not (ANOVA $F_{13,437} = 1.5$, $p = 0.13$). Exponents for small animals ($M <$ CBM) and large animals ($M >$ CBM) are also not heterogeneous (Full-factorial order*CBM*log(M) interactions, $F < 2.0$, $p > 0.16$). After accounting for the effect of M, order has a significant effect on conservative Q_{10}-normalised BMR (ANCOVA $F_{13,453} = 2.1$, $p = 0.02$). However, a Tukey-Kramer H.S.D test reveals that only Chiroptera and Dasyuromorphia are significantly different from each other (Figure 2.8). For small mammals, order has a significant effect on conservative Q_{10}-normalised BMR (ANCOVA $F_{9,302} = 2.9$, $p = 0.004$). *Post hoc* comparison reveals that Chiroptera, Rodentia, and Insectivora each have significantly greater BMRs than Dasyuromorphia (Figure 2.8). For large mammals, order has a significant effect on

Table 2.2. Factorial range (upper limit / lower limit) observed in various measures of residual variation unaccounted for in each of four interspecific regression types.

	total	1 s.d.	95% CI
Unmodified	11.3	1.46	1.030
Conservative	7.8	1.42	1.029
Q_{10} normalised	6.7	1.35	1.027
Cons. Q_{10} normalised	5.7	1.33	1.026

Note to Table 2.2: Details regarding species combinations are provided in the note to Table 2.1.

conservative Q_{10}-normalised BMR (ANCOVA $F_{11,128} = 2.7$, $p = 0.005$). However, *post hoc* comparison was unable to identify where these differences lie (Figure 2.8). Eutheria and Metatheria show significant allometric exponent heterogeneity when conservative Q_{10}-normalised BMRs are compared interspecifically (ANOVA $F_{1,461} = 5.4$, $p = 0.02$) but not interordinally (ANOVA $F_{1,10} = 0.98$, $p = 0.35$). Residuals of Q_{10}-normalised BMRs for

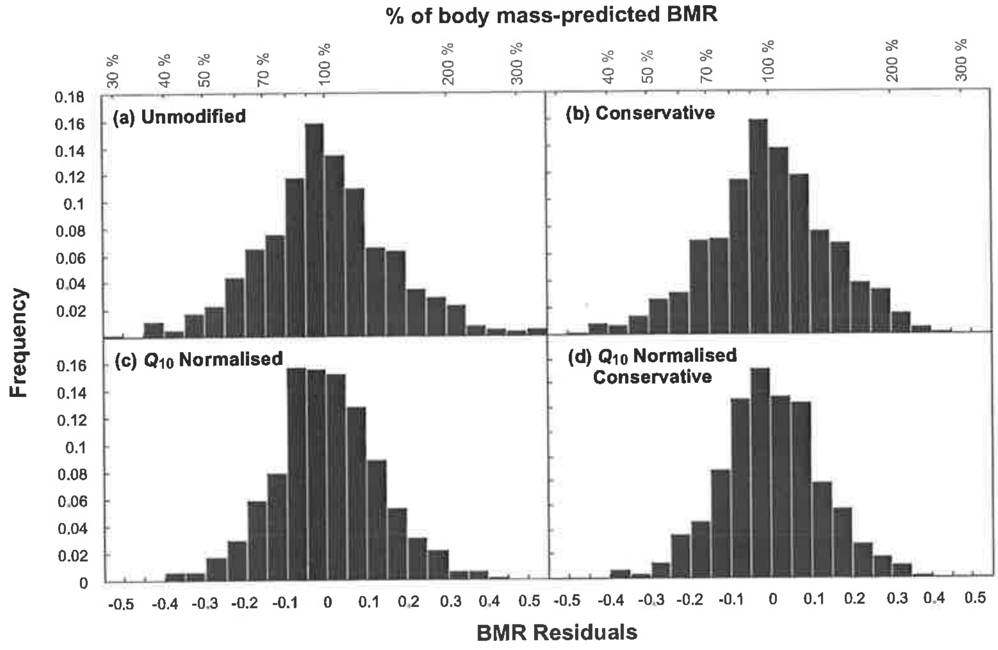

Figure 2.6. Residual variation in mammalian BMR for (a) all data (n = 619), (b) conservative data (n = 571, see methods for selection criteria), (c) all data normalised to a common body temperature of 36.2 °C (n = 507) and (d) conservative data normalised to a common body temperature of 36.2 °C (n = 469).

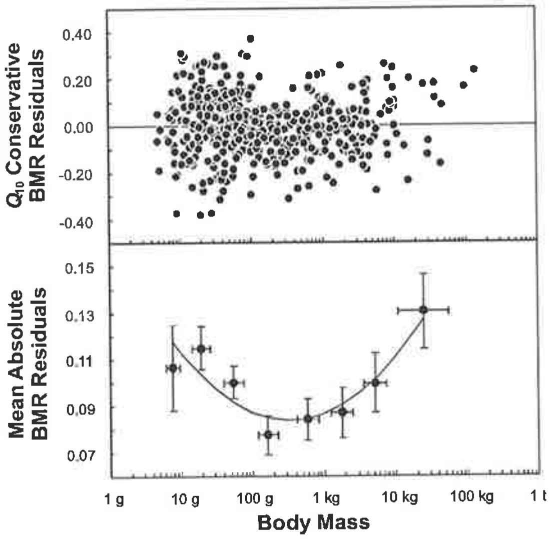

Figure 2.7. Relationship between body mass and the residual variation in mammalian conservative Q_{10}-normalised BMR (top, see methods for selection criteria). Following Lovegrove (2000), mean absolute BMR residuals (bottom) are depicted ± SE, mean body mass values are depicted ± 1 s.d. Variation is maximal at smallest and largest masses. The relationship between the log of body mass (M, g) and mean absolute BMR residuals (Mean Abs. BMR resid = $0.0125 \log(M)^2 - 0.0632 \log(M) + 0.163$, $r^2 = 0.80$) reaches a minimum at 337 g, which is similar to the 358 g reported by Lovegrove (2000).

Eutheria and Metatheria are not significantly different either interspecifically (ANCOVA $F_{1,462} = 2.5$, $p = 0.11$) or interordinally (ANCOVA $F_{1,11} = 0.05$, $p = 0.82$). For small mammals, no significant allometric exponent heterogeneity was identified between zoogeographic regions (ANOVA: region * $\log(M)$ interaction, $F_{4,304} = 0.73$, $p = 0.6$) and region has a significant effect on conservative Q_{10}-normalised BMR (ANCOVA $F_{4,309} = 6.12$, $p < 0.0001$) such that

Neotropical^{a} > Nearctic^{a,b} > Palearctic^{a,b,c} > Afrotropical^{c} > Australian^{c} > Indomalayan^{b,c}

where regions that do not share superscript characters have significantly different mean mass-independent BMRs (Tukey-Kramer H.S.D., $p < 0.05$). Similarly, when zoogeographic regions are compared within the order Rodentia for small species (the only order sufficiently represented in all regions), there is no significant allometric exponent heterogeneity between regions (ANOVA: region * $\log(M)$ interaction, $F_{4,188} = 2.4$, $p = 0.052$) and region has a significant effect on conservative Q_{10}-normalised BMR (ANCOVA, $F_{4,192} = 3.4$, $p = 0.01$) such that

Palaearctic^{a} > Nearctic^{a} > Neotropical^{a,b} > Afrotropical^{b} > Australian^{a,b}

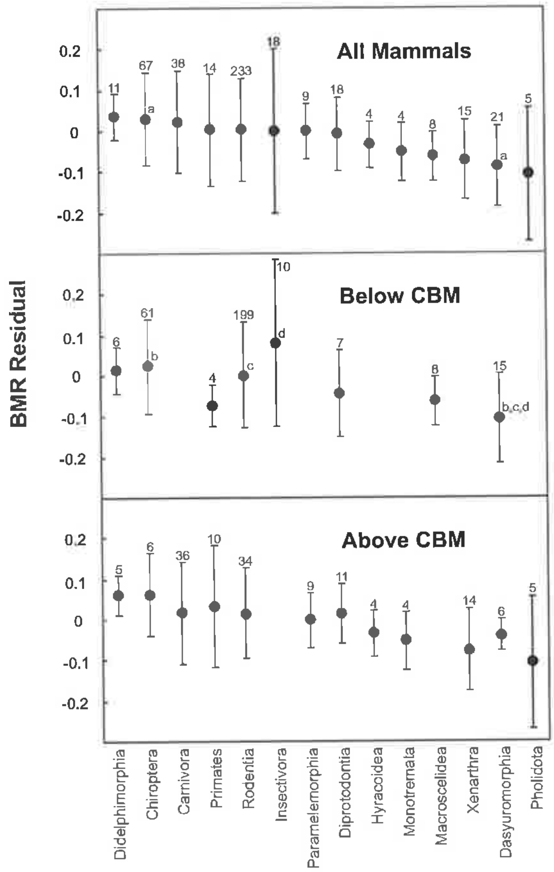

Figure 2.8. Conservative Q_{10}-normalised BMR residuals arranged by order as mean ± s.d of mammals of all sizes (All mammals) or mammals smaller (Below CBM) or larger (Above CBM) than the "constrained body mass" of 350 g (Figure 2.7 and Lovegrove 2000). See methods for details of data selection. Numerals show sample size, lower case characters denote order pairs identified as significantly different (Tukey-Kramer H.S.D. $p < 0.05$).

(Tukey-Kramer H.S.D., $p < 0.05$). For large mammals, however, allometric exponents are significantly heterogeneous between zones (ANOVA: region * log(M) interaction, $F_{4,141} = 3.6$, $p = 0.004$). BMR allometric exponents for these groups differ such that

Palaearctic^{a} > Afrotropical^{a} > Nearctic^{a,b} > Indomalayan^{a,b} > Neotropical^{a,b} > Australian^{b}

where regions that do not share superscript characters have significantly different exponents (assessed using 95% CI overlap). Only the exponents for Palaearctic and Afrotropical mammals differ significantly from 2/3 (assessed using 95% CI overlap, Table 2.3).

Table 2.3. Allometric relationships between mammalian body mass (M, g) and basal metabolic rate (BMR, mL O_2 h^{-1})

	Small Mammals	Large Mammals	All Q_{10} Conservative
Interspecific by Zoogeographic Zone			
Afrotropical	$3.22\,M^{0.71 \pm 0.12}$ (55)	$1.57\,M^{0.80 \pm 0.06}$ (34)	$3.00\,M^{0.72 \pm 0.03}$ (89)
Australian	$4.70\,M^{0.67 \pm 0.07}$ (47)	$4.91\,M^{0.65 \pm 0.06}$ (34)	$3.49\,M^{0.70 \pm 0.02}$ (81)
Indomalayan	$3.42\,M^{0.68 \pm 0.09}$ (11)	$3.71\,M^{0.68 \pm 0.15}$ (14)	$3.20\,M^{0.70 \pm 0.05}$ (25)
Nearctic	$5.46\,M^{0.62 \pm 0.06}$ (90)	$2.74\,M^{0.74 \pm 0.09}$ (21)	$4.52\,M^{0.67 \pm 0.03}$ (111)
Neotropical	$4.99\,M^{0.65 \pm 0.05}$ (77)	$3.95\,M^{0.68 \pm 0.07}$ (43)	$4.96\,M^{0.65 \pm 0.02}$ (120)
Palaearctic	$5.71\,M^{0.61 \pm 0.14}$ (36)	$0.62\,M^{0.94 \pm 0.20}$ (7)	$4.71\,M^{0.66 \pm 0.08}$ (43)
Interspecific by Order			
Carnivora		$1.91\,M^{0.77 \pm 0.07}$ (36)	$2.84\,M^{0.73 \pm 0.06}$ (38)
Chiroptera	$4.13\,M^{0.70 \pm 0.07}$ (61)		$4.10\,M^{0.70 \pm 0.05}$ (67)
Dasyuromorphia	$3.07\,M^{0.70 \pm 0.16}$ (15)	$3.07\,M^{0.71 \pm 0.12}$ (6)	$2.92\,M^{0.71 \pm 0.05}$ (21)
Didelphimorphia	$2.97\,M^{0.76 \pm 0.09}$ (6)		$3.29\,M^{0.73 \pm 0.05}$ (11)
Diprotodontia	$5.65\,M^{0.56 \pm 0.25}$ (7)	$8.41\,M^{0.59 \pm 0.10}$ (11)	$3.92\,M^{0.68 \pm 0.04}$ (18)
Insectivora	$4.36\,M^{0.72 \pm 0.5}$ (10)		$6.88\,M^{0.57 \pm 0.14}$ (18)
Monotremata		$1.22\,M^{0.82 \pm 0.19}$ (4)	$1.22\,M^{0.82 \pm 0.19}$ (4)
Primates	$12.58\,M^{0.44 \pm 0.35}$ (4)	$1.21\,M^{0.84 \pm 0.20}$ (10)	$1.88\,M^{0.79 \pm 0.10}$ (14)
Rodentia	$5.23\,M^{0.62 \pm 0.05}$ (199)	$2.48\,M^{0.75 \pm 0.08}$ (34)	$4.33\,M^{0.67 \pm 0.03}$ (233)
Xenarthra		$3.14\,M^{0.69 \pm 0.14}$ (14)	$3.74\,M^{0.67 \pm 0.11}$ (15)

Note to Table 2.3: All regressions are based on BMR data normalised to a T_b of 36.2 °C with data for Lagomorpha, Artiodactyla, Soricidae (Insectivora), and Macropodidae (Diprotodontia) excluded (sample size in parentheses). Regression exponents are presented ± 95% CI. Small mammals are those < 350 g, large mammals are > 350 g. 350 g is the 'constrained body mass' identified by analysis of BMR residuals (see Figure 2.7).

Correlates to BMR

BMR residuals may be compared to residuals for a variety of physiological, ecological, and life-history variables to test hypothesised correlations. Significant correlations ($p < 0.05$, Table 2.4) exist between BMR residuals and residuals for FMR (Mammalia and Rodentia), cold-induced MMR (Mammalia and Rodentia), resting heart rate (Mammalia and Diprotodontia), population density (Carnivora), lifespan (Carnivora and Dasyuromorphia), litter size (Mammalia, Dasyuromorphia, and Macroscelidae), litters produced per year (Carnivora), and annual fecundity (Rodentia). Only body surface area and exercise-induced MMR were not significantly correlated with BMR within either Mammalia or at least one of the orders examined ($p > 0.05$, Table 2.4).

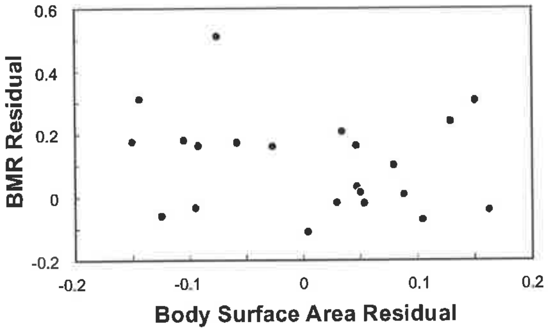

Figure 2.9. Interspecific relationship between mass-independent residuals of basal metabolic rate (BMR) and body surface area. The correlation is not significant (r = -0.22, p = 0.31, n = 22).

Discussion

Allometry of mammalian BMR

Body mass accounts for 94% of the variation in mammalian BMR before correction for T_b and digestive state (Table 2.1). Normalisation to a common T_b cuts the residual variation in BMR in half (Table 2.2). Following exclusion of likely non-basal measurements (Artiodactyla, Soricidae, Macropodidae and Lagomorpha), M accounts for 96% of the interspecific variation and 99% of the interordinal variation in Q_{10}-normalised BMR (Table 2.1). No significant allometric exponent heterogeneity is evident between orders, and only large Palaearctic and Afrotropical species scale with an exponent different from 2/3. The general conclusion is therefore that BMR of mammals is proportional to $M^{2/3}$, which is also the case for birds (Bennett and Harvey 1987; Reynolds and Lee 1996; Tieleman and Williams 2000; Frappell *et al.* 2001).

The usual interpretation of a 2/3 scaling exponent for BMR is that it reflects a balance between the production of heat through metabolic processes and the loss of heat through the body surface, which is also proportional to $M^{2/3}$ (Reynolds 1997). Although this hypothesis can not be rejected, it is not supported by the relationship between the residuals of BMR and body surface area (Figure 2.9). Similarly, Holloway and Geiser (2001) found no difference between the resting metabolic rates of sugar gliders (*Petaurus breviceps*) in helox (79% helium, 21% oxygen) and normal atmospheres despite observing a significant increase in

Table 2.4. Interspecific residual (body mass-independent) correlations between BMR and selected physiological, ecological and life-history parameters in mammalian groups

	Mam	Car	Chi	Das	Did	Dip	Ins	Mac	Rod	Xen
Body Surface Area	-0.2 (22)	0.9 (3)				0.81 (4)	0.1 (3)		-0.1 (7)	
Population Density		-0.4* (25)		-0.6 (3)	0.8 (3)	-0.5 (8)	-0.6 (7)		0.3 (70)	-0.1 (4)
Fecundity	0.2 (78)	-0.3 (17)	0.6 (5)	-0.2 (4)	0.8 (3)	0 (4)	-0.3 (6)		0.4* (28)	0.6 (6)
FMR	0.7*** (30)		0.7 (5)			0.92 (4)			0.9*** (11)	
Heart Rate	0.5*** (48)	0.2 (11)	-0.1 (3)	0.7 (5)		0.95* (5)			0.2 (17)	
Lifespan	-0.1 (225)	-0.3* (40)	0 (15)	-0.7** (13)	0.9 (4)	-0.7** (14)	0.1 (11)		-0.3* (78)	-0.4 (11)
Litter Size	0.2* (198)	0.2 (28)	-0.5 (5)	0.5* (20)	-0.1 (10)	-0.4 (12)	0.2 (21)	-0.97* (4)	0.2 (66)	0.2 (12)
Litters per Year	0.1 (78)	-0.5* (17)	0.8 (6)	-0.5 (4)	-0.3 (3)	-0.2 (4)	-0.3 (7)		0.3 (26)	0.4 (6)
MMR – Cold	0.4** (56)			0 (6)		0.84 (5)			0.4* (41)	
MMR – Exercise	0.3 (21)	0.3 (4)							0.3 (16)	

Note to Table 2.4: Data sorted into the following taxonomic groups: All mammals (Mam); Carnivora (Car); Chiroptera (Chi); Dasyuromorphia (Das); Didelphimorphia (Did); Diprotodontia (Dip); Insectivora (Ins); Macroscelidae (Mac); Rodentia (Rod); Xenarthra (Xen). Data for some orders are not presented due to small sample size and lack of significance, therefore n values may not sum across rows. Data were compiled from published sources (Appendix A, Kinnear and Brown 1967; Dawson and Hulbert 1970; Eisenberg 1981; Seeherman *et al.* 1981; Taylor *et al.* 1981; Maloiy *et al.* 1982; Müller *et al.* 1983; MacArthur 1984; Damuth 1987; Koteja 1987; Bozinovic 1992; Hinds and Rice-Warner 1992; Van Tienhoven *et al.* 1993; Chappell and Dawson 1994; Nagy 1994; Purvis and Harvey 1995; Reynolds 1997; Symonds 1999; Carey and Judge 2000; Nagy and Bradshaw 2000; Barros *et al.* 2001; Holloway and Geiser 2001; Nespolo *et al.* 2001). Superscripts denote significance: (0.05, 0.01, and 0.001 for *, **, and ***, respectively), sample size in parentheses.

thermoneutral thermal conductance in the helox atmosphere. They concluded that an animal's rate of basal energy expenditure is not related to heat loss, which suggests that surface area and BMR need not be causally related.

Variation in BMR between taxa

Despite the improvement of allometry, variation about the regression line remains considerable, particularly between species (Figure 2.6, Table 2.2). Despite this variation, scaling exponents do not differ, either between orders or between Eutheria and Metatheria, suggesting that deviations from a BMR scaling exponent of 2/3 that occur at the level of class, infraclass and order are a result of T_b variation that is correlated with M. Differences in BMR scaling between eutherians and metatherians, for example, can be accounted for by the lower T_b of metatherians coupled with different relationships between T_b and M (Chapter 1). Furthermore, across Mammalia only the orders Chiroptera and Dasyuromorphia have significantly different BMRs (Figure 2.8). However, small (< 350 g) dasyuromorph marsupials have significantly lower BMRs than small rodents, bats and insectivores (Figure 2.8).

Given that avian and mammalian endothermy almost certainly evolved separately, it would be interesting to determine if the BMR differences between mammals and birds can be similarly accounted for by the differences in body temperature between these groups (McNab 1966a). As a preliminary investigation of this possibility, BMR and T_b data were collated for 66 species of bird (Daan *et al.* 1989; Thouzeau *et al.* 1999; McNab 2000a; Tieleman and Williams 2000; Frappell *et al.* 2001; McKechnie and Lovegrove 2001; 2003). As expected, BMR scaling exponents do not differ between mammals and birds and birds have higher BMRs than mammals (Figure 2.10a). A Q_{10} of 3.0 was then used to normalise the BMRs of birds and mammals to a common T_b. This Q_{10} was chosen because it minimises variation in mammalian Q_{10}-normalised BMR (Chapter 1). However, mammalian mass-independent conservative BMR (mL O_2 $g^{-0.67}$ h^{-1}) is related to T_b with a Q_{10} of 2.8 (Figure 2.11). Q_{10} has a quantifiable effect on the scaling exponent, but the difference between Q_{10} values of 2.8 and 3.0 is minor, and b is not significantly different from 2/3 within the range of $2.0 \geq Q_{10} \geq 4.0$ (Figure 2.12). When normalised to a T_b intermediate between birds and mammals (38.2 °C, $Q_{10} = 3.0$), scaling exponents for these groups do not differ and birds and mammals do not have significantly different BMRs (Figure 2.10b). This similarity between the BMRs of birds and mammals further supports the suggestion that a common cause underlies the influence of M on BMR for endothermic homeotherms (Chapter 1).

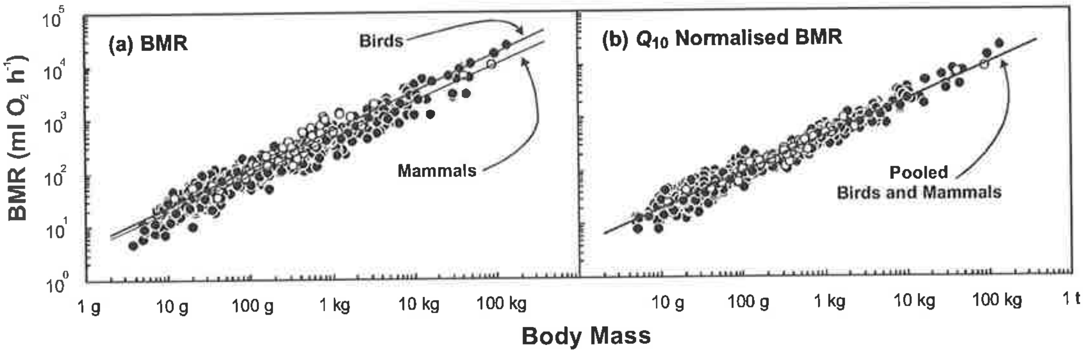

Figure 2.10. Relationship between body mass and basal metabolic rate (a, BMR) or Q_{10}-normalised BMR (b) for birds (unfilled symbols) and mammals (filled symbols). Regression lines are shown extrapolated beyond data ranges to facilitate comparison. Q_{10}-normalised BMRs were normalised to a body temperature of 38.2 °C, which is intermediate between the mean (± s.d.) body temperatures of birds (40.1 ± 1.9, n = 86) and mammals (36.2 ± 1.9, n = 507). A Q_{10} of 3.0 was used for all calculations. Scaling exponents for bird and mammal BMR do not differ (ANOVA $F_{1,633} = 0.72$, $p = 0.40$) and birds have higher BMRs than mammals (ANCOVA $F_{1,633} = 43.5$, $p < 0.0001$). Bird and mammal Q_{10}-normalised BMRs do not have different scaling exponents (ANOVA $F_{1,512} = 0.11$, $p = 0.74$) or elevations (ANCOVA $F_{1,513} = 0.11$, $p = 0.74$). Equations of the regression lines: Bird BMR $= 4.58\,M^{0.71}$, $r^2 = 0.91$, n = 66; Mammal BMR $= 3.98\,M^{0.69}$, $r^2 = 0.94$, n = 469; Q_{10}-normalised BMR $= 4.16\,M^{0.68}$, $r^2 = 0.96$.

Correlates to BMR

Independent of body mass, high BMR is associated with high maximum and field metabolic rates, high resting heart rates, production of large numbers of offspring per litter, low population density, and short lifespans (Table 2.4). The number and variety of variables with which BMR is significantly correlated suggests that, despite being an unnatural physiological construct that animals rarely show under natural conditions, BMR does indeed contain a useful and meaningful signal.

If BMR is considered to be the minimum energy cost of maintaining the body, its level is likely to be related to the capacity of the body for activity. Animals with higher aerobic capacities have higher mitochondrial volumes (Mathieu *et al.* 1980; Hoppeler 1990), and this in turn is related to greater proton leakage through mitochondrial membranes, which is a significant component of metabolic rate (Hulbert and Else 2000). Similarly, BMR and MMR residuals are positively correlated when elicited both by cold exposure and exercise, although only the former was significant in this analysis (Table 2.4). Previous work provides

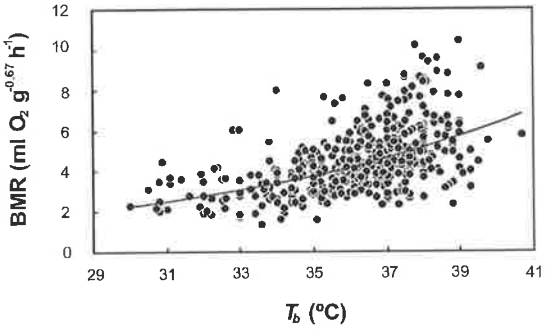

Figure 2.11. Relationship between body temperature (T_b, °C) and mass-independent conservative Q_{10}-normalised BMR (mL O$_2$ g$^{-0.67}$ h^{-1}). Equation of the regression line: BMR = $0.0987\ e^{(0.104\ T_b)}$. T_b and BMR are therefore related with a Q_{10} of $e^{(0.104 \times 10)}$, or 2.8 (see Appendix B for derivation of Q_{10} calculation).

mixed support for a correlation between MMR and BMR (reviewed by Hayes and Garland 1995). Significant interspecific and intraspecific correlations have been reported within Mammalia, both for cold-induced and exercise-induced MMR, although such relationships are not ubiquitous and have not been demonstrated for all species or clades so far investigated (Hayes and Garland 1995). This is particularly true of broad, interspecific studies such as the present one, where measurements have been obtained by a variety of experimenters using a range of methodologies (e.g. Koteja 1987). In such cases metabolic data may not be strictly comparable (Hayes *et al.* 1992b) and elucidation of significant relationships becomes increasingly difficult.

Given that the physiological and biochemical processes that contribute to BMR continue under field conditions, and that BMR is equal to around 20 - 35% of FMR (calculated using Figure 2.2d and Nagy *et al.* 1999), it is also reasonable to assume that an animal with a high basal energy expenditure would have a high field rate of energy expenditure. In support of this suggestion, FMR residuals are positively correlated with BMR residuals within both Mammalia and Rodentia (Table 2.4).

Within Mammalia and Diprotodontia, BMR residuals are significantly positively correlated with heart rate (HR) residuals (Table 2.4). This original interspecific analysis therefore supports the same pattern shown intraspecifically in studies designed to estimate field metabolic rate indirectly by measuring HR with radio-telemetry (e.g. Froget *et al.* 2001; McCarron *et al.* 2001; Butler *et al.* 2002). Such correlations are theoretically expected, because they are based on the Fick principle. HR is also thought to be related to lifespan:

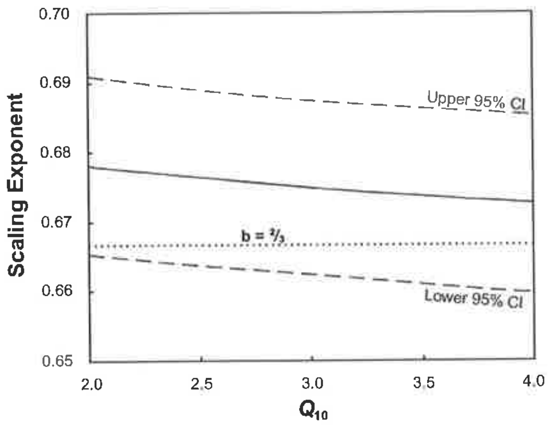

Figure 2.12. Effect of altering Q_{10} on the scaling exponent (b, where BMR = a M^b, BMR is basal metabolic rate, and M is body mass) estimated for mammalian conservative Q_{10}-normalised BMR. Within the range of $2.0 \geq Q_{10} \geq 4.0$, b (represented by the solid line) is not significantly different from 2/3. Broken lines represent the upper and lower 95% confidence limit of the scaling exponent; the dotted line represents an exponent of 2/3. A Q_{10} of 3.0 was used for normalisation to a common T_b throughout this study and Chapter 1. A Q_{10} of 2.8 is suggested by the relationship between mass independent BMR and T_b (assuming a b value of 2/3, Figure 2.11).

large animals live longer than small ones, but do so at a slower rate, so the total number of heart beats throughout an animal's life is expected to be roughly independent of body mass (Schmidt-Nielsen 1984; 1990). However, the product of HR and lifespan scales with a negative exponent and HR and lifespan residuals are not significantly correlated ($r = 0.07$, $n = 45$, $p = 0.65$; HR [beats year^{-1}] = $6.4 \times 10^8 M^{-0.29}$, $r^2 = 0.80$; max recorded lifespan [years] = $2.0 M^{0.22}$, $r^2 = 0.45$; sources presented in Table 2.4). Large animals therefore experience fewer heartbeats in their lives than small animals and species with long lifespans do not experience a greater number of heartbeats than short-lived ones. This suggests that lifespan and HR are related only as a consequence of body size. However, maximum recorded lifespan is a poor measure of natural longevity (Speakman *et al.* 2002), and the trend for larger animals to show fewer heartbeats in their lifetimes may simply be a reflection of the relative difficulty of obtaining reliable maximum lifespan data for larger animals (Calder 1984). The failure to identify a significant correlation between BMR and lifespan residuals across Mammalia may also stem from similar problems (Table 2.4). Within Carnivora, Dasyuromorphia, Diprotodontia and Rodentia, however, BMR and lifespan are significantly negatively correlated (Table 2.4). In further support of the 'rate-of-living' or 'live fast, die young' hypothesis (reviewed by Speakman *et al.* 2002), lifespan residuals are significantly negatively correlated with residuals for litter size ($r = -0.46$, $n = 153$, $p < 0.0001$), litters per year ($r = -0.36$, $n = 68$, $p = 0.003$), and annual fecundity ($r = -0.59$, $n = 65$, $p < 0.0001$) across Mammalia. Assuming that reproductive lifespan is related to maximum lifespan, lifetime reproductive output (calculated as the product of lifespan and fecundity) is body size invariant (log-log transformed, $r = 0.15$, $n = 65$, $p = 0.22$). Short-lived species therefore compensate for their lack of longevity with an increased rate of offspring production, and thereby produce a similar number of offspring as long-lived species. The product of lifespan and BMR, on the other hand, scales with an exponent significantly less than 1 ($b = 0.90$, 95% CI: 0.86 – 0.94, $n = 224$), which suggests that large animals use less energy per kg of body mass over their lifetimes than small ones. Once again, this may also reflect the difficulty of obtaining reliable maximum lifespan data for larger animals (Calder 1984).

BMR and FMR are significantly positively correlated, so a low population density might be expected for animals with high BMRs, because they are likely to require a greater quantity of resources than those with low BMRs. However, BMR and population density residuals are correlated only within Carnivora (Table 2.4). Nevertheless, home range scaling exponents estimated according to Haskell *et al.* (2002) are closer to measured values when a BMR scaling exponent of 2/3 is used in preference to 3/4 (Chapter 1).

Studies on the relationship between BMR and other life-history characteristics provide mixed results. Read and Harvey (1989) and Harvey *et al.* (1991) compared mass-independent measures of BMR with mass-independent measures of multiple reproductive variables across eutherian orders and found no significant correlations, except one: in accord with this study (Table 2.4), they found that variation in litter size was positively correlated with BMR. Conversely, Cruz-Neto and Jones (in press) concluded that the evolution of low BMRs within Chiroptera was correlated with faster life histories (earlier age at maturity and higher rates of mortality) and BMR and fecundity were significantly correlated only if the influence of body mass was not removed. Similarly, Symonds (1999) found that within Insectivora, BMR was significantly negatively correlated with gestation length, the period of maternal investment, maximum lifespan, and maximum reproductive lifespan. No significant correlation between litter size and BMR was identified within Insectivora (Symonds 1999). Intraspecifically, BMR and life-history variables are uncorrelated for *Sigmodon hispidus* (Derting and McClure 1989), *Peromyscus maniculatus* (Earle and Lavigne 1990), *Mus musculus* (Hayes *et al.* 1992a; Johnson *et al.* 2001), *Microgale dobsoni* (Stephenson and Racey 1993b) and *Geogale aurita* (Stephenson and Racey 1993b). Laboratory raised lines of mice divergently selected for heat loss measured by direct calorimetry, on the other hand, have shown a positive correlation between resting metabolic rate and litter size associated with a similar change in ovulation rate (Nielsen *et al.* 1997). Similarly, mice selected for high rates of food intake have high RMRs (Selman *et al.* 2001a), high ovulation rates (Brien *et al.* 1984) and produce large litters (Brien *et al.* 1984) relative to control lines and lines selected for low rates of food intake. The positive correlation between BMR and litter size observed across Mammalia (Table 2.4) is therefore also likely to be associated with a positive correlation between BMR and ovulation rate.

It is clearly unrealistic to expect that BMR can be shown to be correlated with all physiological and ecological characteristics of mammals, but in view of the natural and experimental variation in the available data, the appearance of many significant correlations of residuals shows that BMR contains a relatively high signal-to-noise ratio. Because BMR is a relatively simple measurement to make, it therefore remains a practical metric of metabolic intensity of animals and will continue to be a central benchmark in comparative physiology.

Acknowledgements

The paper from which this chapter sprung was first presented during the "What is BMR/SMR and is it a useful concept?" symposium at the 6th International Congress of Comparative Physiology and Biochemistry. I am grateful to Pat Butler and Tobias Wang both for organising the symposium, and for allowing me to speak. The chapter benefited greatly from the discussions that followed. I therefore also thank Frank Bonaccorso, Ariovaldo Cruz-Neto, Frank Fish, Peter Frappell, Fritz Geiser, Ian Hume, Marek Konarzewski, Harvey Lillywhite, Barry Lovegrove, Brian McNab and Phil Withers for thought provoking and entertaining discussions about the usefulness of BMR. Barry Lovegrove and Brian McNab provided comments that greatly improved a draft version of this chapter.

3. Interindividual metabolic rate and cost of transport variation in an Australian murid rodent, the spinifex hopping mouse *Notomys alexis*

Abstract

Studies of mammalian basal metabolic rate (BMR) generally either focus on the interspecific relationship between BMR and body mass or attempt to explain the adaptive significance of BMR differences between species. However, analysis of interspecific data both neglects considerable interindividual variation and conceals in averages the variation on which natural selection acts. This chapter assesses intraspecific variation in a range of physiological variables in an Australian murid rodent, *Notomys alexis*. Variables measured were BMR, wet thermal conductance, lower critical temperature of the thermoneutral zone, body temperature, exercise-induced maximum metabolic rate, burrowing metabolic rate, maximum running speed, maximal aerobic speed, burrowing speed, and the net costs of transport by burrowing and running. Most variables were significantly repeatable, suggesting that individual measurements were reliable. Mean values were similar to values predicted by allometry, but variation between individuals was considerable and in some cases exceeded 50% of that observed between species. Nine of 55 possible intraspecific correlations were significant, but BMR was significantly correlated only with wet thermal conductance, which suggests that BMR is influenced by heat loss. Wet thermal conductance was also significantly correlated with body temperature, lower critical temperature and maximal aerobic speed. Maximal aerobic speed was also significantly correlated with body temperature and net cost of pedestrian transport. Body temperature was significantly correlated with net cost of pedestrian transport, burrowing speed was significantly correlated with maximum running speed, and lower critical temperature was significantly correlated with burrowing metabolic rate. Burrowing locomotion is more expensive than for specialised fossorial species, but the high terrestrial speeds afforded by saltatory locomotion outweigh the energetic savings associated with burrowing specialisation.

Introduction

Mammalian basal metabolic rate (BMR, mL O_2 min^{-1}) is one of the most widely measured physiological metrics, with the nature and causes of the interspecific relationship between body mass (M, g) and BMR continuing to be investigated and debated (Chapters 1, 2, and 7;

West *et al.* 1997; 1999; Darveau *et al.* 2002; Symonds and Elgar 2002). However, interspecific analyses neglect considerable variation within species and are complicated by the hierarchical nature of phylogenetic descent, which means that species values are not necessarily statistically independent points on which comparison can be based (Felsenstein 1985; Harvey and Pagel 1991; Garland *et al.* 1993). While the analysis of interspecific data has been the mainstay of comparative and ecological physiology throughout most of its history and is likely to continue to provide valuable insight into the selective forces that shape organisms, the attention of physiologists has now expanded to include analysis of interindividual variation (e.g. Bennett 1987; Hayes *et al.* 1992a; Konarzewski and Diamond 1994; 1995; Chappell and Bachman 1995; Berteaux *et al.* 1996; Berteaux and Thomas 1999; Dohm *et al.* 2001; Speakman *et al.* 2003). Analyses of this sort are not encumbered by the statistical problems associated with shared descent and are appropriately focused to infer adaptation, the ultimate source of which must be selection on traits within populations (Bennett 1987).

For a trait to evolve it must be heritable, there must be consistent (i.e. repeatable) variation in the trait, and this variation must be capable of influencing the fitness of individuals. Estimates of repeatability provide information about the stability of a given trait through time and can also provide some information about heritability (Dohm 2002). Repeatability estimates for BMR are available only for house mice (Dohm *et al.* 2001) and two species of bird (Bech *et al.* 1999; Horak *et al.* 2002). In each case, BMR is significantly repeatable, as is resting metabolic rate (MR) of kangaroo rats (Hayes *et al.* 1998). Intraspecific BMR is also quite variable. The coefficient of variation for BMR of genetically variable outbred house mice is ca. 20% (Dohm *et al.* 2001) and that for resting MR of birds is 4.5% to 21% (Burness *et al.* 1998). Although originally conceived as the minimum level of metabolism compatible with existence (Kleiber 1961), the wide variability observed in BMR suggests functional significance. The adaptive significance of BMR variation has been repeatedly inferred interspecifically (e.g. Chapters 2 and 4, Hayssen and Lacy 1985; Elgar and Harvey 1987; McNab 1988a; Konarzewski and Diamond 1995; Lovegrove *et al.* 2001; Mueller and Diamond 2001; Lovegrove 2003), but the search for intraspecific correlations between BMR and other variables has provided mixed results. For example, variation in BMR is correlated with the mass of metabolically active organs (Konarzewski and Diamond 1994), but not with life history variables in domestic mice (Hayes *et al.* 1992a); the resting MR of ground squirrels is significantly correlated with exercise-induced maximum MR, but not thermogenic maximum MR (Chappell and Bachman 1995); and resting MR of meadow voles is significantly correlated with daily energy expenditure (Speakman *et al.* 2003), but this correlation is associated with differences between field sites and was not evident within sites.

This study assesses variation in BMR and a range of other physiological variables in the spinifex hopping mouse, *Notomys alexis*. Traits measured include BMR, wet thermal conductance, lower critical temperature of the thermoneutral zone, body temperature, exercise-induced maximum metabolic rate, burrowing metabolic rate, maximum running speed, maximal aerobic speed, burrowing speed, and the net costs of transport by burrowing and running. *N. alexis* was selected as a study species because information is already available on basal and maximal metabolism (MacMillen and Lee 1970; Hinds and Rice-Warner 1992), thermoregulation (MacMillen and Lee 1970) and locomotion (Baudinette *et al.* 1976; Garland *et al.* 1988). These published data are used to evaluate the reliability of means from this study, as are allometric predictions based on interspecific correlations. The functional and adaptive significance of interindividual variation in BMR is assessed by intraspecific correlation with the ten other physiological variables. Additionally, each of these ten variables is compared with the remaining nine, allowing for examination of a further 45 intraspecific correlations.

This study also includes the first measurement of burrowing net cost of transport for a semi-fossorial (burrowing, but surface-foraging) mammal. Burrowing costs are compared between this species, which is adapted to saltation, and species that are adapted to burrowing. Total burrow construction costs are also compared between fossorial and semi-fossorial mammals.

Methods

Study species

Eleven adult spinifex hopping mice (6 male, 5 female, mean mass 33.0 g), *Notomys alexis* (Rodentia: Muridae), were obtained from a captive colony maintained by the Department of Anatomical Sciences at The University of Adelaide.

Mice were housed either individually or in single sex groups of three in an air-conditioned animal housing facility at the North Terrace campus of the University of Adelaide at a temperature of 22 - 26 °C and maintained on an *ad libitum* diet of mixed grains supplemented with fresh fruit. Water was available at all times. All animals maintained body weight under these conditions.

Body temperature

For measurements of body temperature (T_b, °C), animals were weighed and restrained by hand in a cheesecloth bag to minimise heat transfer. The base of the tail was then exposed and T_b was measured by inserting a fine-gauge thermocouple ~5 mm into the rectum. The K-type thermocouple was connected to a Fluke model 52 thermometer (John Fluke MFG. Co. Inc., Everett, Washington) that was calibrated to ± 0.1 °C with a certified mercury thermometer. Data were disregarded if the mouse struggled against restraint.

Resting $\dot{V}O_2$

The rate of oxygen consumption ($\dot{V}O_2$, mL min^{-1}) of resting, postabsorptive (fasted 6+ h), nonreproductive mice was measured during daylight hours using positive pressure open flow respirometry according to standard techniques (Withers 2001). Air drawn from outside was pumped through a pressure regulator and a series of absorbent tubes (Drierite™, self-indicating soda lime, and Drierite) to provide a dry, CO_2-free airstream. This airstream was then split four ways to provide a single reference stream and three animal streams. Each of the animal streams passed through a 0-1 L min^{-1} mass-flow controller (Sierra Instruments Mass-Trak model# 810C-DR-13; calibrated with a Brooks Vol-U-Meter) at a rate of 500 - 750 mL min^{-1}, 1 m of temperature equilibration tubing, a 765 mL animal chamber and a respirometry multiplexer that sequentially selected each of the four streams for a user-specified period (usually 10 min). A subsample of the multiplexer outflow was passed through a small U-tube containing Drierite, Ascarite™, and Drierite, and into a Sable Systems Oxzilla™ dual absolute and differential oxygen analyser, calibrated with outside air (0.2095 O_2). The temperature equilibration tubing and respirometry chamber were contained within a constant temperature cabinet stable to ± 1 °C, the temperature of which was measured with a precision mercury thermometer (T_a, °C). The voltage output of the oxygen analyser was connected to a PC compatible computer via a Sable Systems Universal Interface analogue/digital converter. Sable Systems DATACAN V5.2 data acquisition software sampled the analyser output at a rate of 3 Hz and averaged three samples to generate each recorded point.

Measurements of resting $\dot{V}O_2$ were obtained at T_a ranging from 5 - 36 °C. Animals were observed in the respirometer and periods of inactivity were noted; data were accepted if

$\dot{V}_{O_2}$ remained low and stable for more than 5 min. The thermoneutral zone was defined as the T_a range over which $\dot{V}_{O_2}$ was independent of T_a. BMR was calculated as average $\dot{V}_{O_2}$ within the thermoneutral zone, wet thermal conductance (C_{wet}, mL O_2 min^{-1} °C^{-1}) was calculated as the absolute slope of the line relating $\dot{V}_{O_2}$ and T_a below the zone of thermoneutrality, and lower critical temperature (T_{lc}, °C: lower limit of the zone of thermoneutrality) was calculated by determining the T_a at which the line relating $\dot{V}_{O_2}$ and T_a below the zone of thermoneutrality was equal to BMR.

Exercise $\dot{V}_{O_2}$

A negative pressure respirometry system was used to measure $\dot{V}_{O_2}$ of active animals while running or burrowing. Air was drawn with a Reciprocator piston pump (Selby Scientific, Clayton, Victoria, Australia) through a running chamber or a burrowing tube (see below), through a 0-10 L min^{-1} mass-flow meter (Sierra Instruments Top-Trak model# 822-13-OV1-PV1-V1 calibrated with a Brooks Vol-U-Meter). A subsample of this air was then passed through a small U-tube containing either Drierite (for running and burrowing net cost of transport) or Drierite-Ascarite-Drierite (for exercise $\dot{V}_{O_2\text{max}}$), and into the system described above.

To determine the maximum exercise metabolic rate of mice ($\dot{V}_{O_2\text{max}}$, mL min^{-1}) air was drawn at a rate of 5 - 6 L min^{-1} through a 1.5 L running chamber resting on a motorised treadmill at speeds of 5 - 60 m min^{-1}. Starting at the lower speeds, mice were run until $\dot{V}_{O_2}$ stabilised, at which time treadmill speed was increased in intervals of 10 – 20 m min^{-1} until further increases in speed no longer resulted in increased $\dot{V}_{O_2}$ (Figure 3.1). $\dot{V}_{O_2\text{max}}$ was then calculated as the average of the stable plateau $\dot{V}_{O_2}$ (Figure 3.1). NCOT$_p$ was calculated by multiplying the slope of the line relating $\dot{V}_{O_2}$ (mL min^{-1}) and speed (m min^{-1}) by the energy equivalent of 1 mL of O_2 (20.5 J: Withers 1992), assuming a respiratory quotient (RQ) of 0.8, which minimises error in the calculated rate of energy use (Koteja 1996). Maximum aerobic speed (U_{ma}, m min^{-1}) was calculated by determining the speed at which the line relating $\dot{V}_{O_2}$ and speed was equal to $\dot{V}_{O_2\text{max}}$.

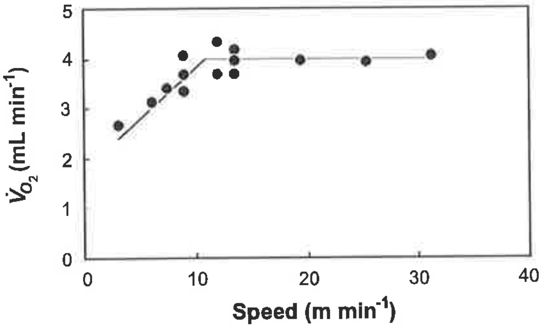

Figure 3.1. Relationship between metabolic rate ($\dot{V}_{O2}$, mL min^{-1}) and speed (m min^{-1}) for a single male hopping mouse (M = 31.5 g). The break-point of the regression relating $\dot{V}_{O_2}$ and speed is equal to maximum aerobic speed (U_{ma}, m min^{-1}). At speeds less than U_{ma}, the slope of the line relating $\dot{V}_{O_2}$ and speed is equal to the net O_2 cost of transport (mL O_2 m^{-1}), which can be converted to the net cost of pedestrian transport (NCOT$_p$, J m^{-1}) by assuming a RQ of 0.8 (1 mL O_2 = 20.5 J: Withers 1992). Average $\dot{V}_{O_2}$ at speeds greater than U_{ma} is equal to maximum metabolic rate ($\dot{V}_{O_2\max}$, mL min^{-1}).

To determine the net cost of transport by burrowing (NCOT$_b$, J m^{-1}), mice were placed in a chamber similar to that used by Vleck (1979), who made the first measurements of burrowing energetics of a mammal. The chamber consisted of a 40 cm long clear acrylic tube (11 cm i.d.) filled with soil to a distance of ~35 cm from the terminal end (Figure 3.2). A 10 cm diameter PVC T-junction was fixed to the open end of the tube. The animal could be placed in the chamber through the threaded lid on the end branch, and the spoil fell through a wire mesh on the lower branch (Figure 3.2). Prior to being placed in the tube, soil (80:20 sand and loam mix) was moistened until it was cohesive enough to stick together when squeezed by hand. The total mass of moist soil (± s.d.) averaged 5.1 ± 0.6 kg, and density averaged 1.5 g cm^{-3}. Equilibration time for the burrowing system was estimated at around 5 min from examination of experimental traces (e.g. Figure 3.3) and was calculated at 2 – 12 min depending on flow rate (1.5 – 2 L min^{-1}), the amount of mixing occurring within the system, and assuming a soil air-filled porosity of 0.3 (total volume of air in the system was equal to approximately 3.3 L). Time to equilibration was considerably less than the time spent burrowing during a typical trial (mean burrowing duration ± s.d. = 27 ± 16 min). Burrowing mouse $\dot{V}_{O_2}$ ($\dot{V}_{O_2b}$, mL min^{-1}) was determined by subtracting soil $\dot{V}_{O_2}$ from the combined $\dot{V}_{O_2}$ of mouse and soil. Soil $\dot{V}_{O_2}$ (0.09 ± 0.05 mL O_2 min^{-1}) averaged only 2% of mouse burrowing $\dot{V}_{O_2}$. Burrowing speed (U_b, m min^{-1}) was calculated by dividing distance burrowed by total time spent burrowing and NCOT$_b$ was then determined by dividing $\dot{V}_{O_2b}$ by U_b.

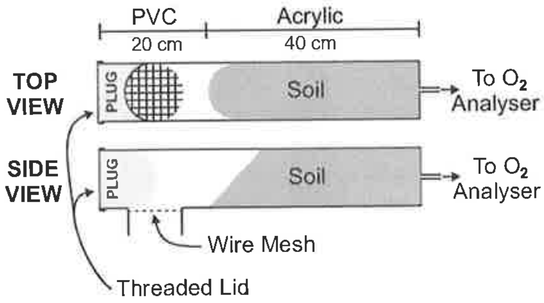

Figure 3.2. Diagrammatic representation of the chamber used for measurement of burrowing $\dot{V}O_2$.

Maximum running speed

Maximum running speed (MRS, m s^{-1}) was measured using a series of six infra-red light gate stations placed opposite reflectors at 20 cm intervals along the central portion of a 2.5 m long raceway, 20 cm in width and with a rubberised floor for traction. The five stations were star-connected to a PC interface unit that supplied power to the stations via the signal lines and was connected to a Toshiba T3300SL laptop computer via the IEEE parallel port. Each station comprised six 900 nm infra-red LEDs housed in tubes for collimation and eight detectors sensitive to such light. The LEDs and detectors were arranged vertically with four of the detectors closely spaced near the floor of the raceway (interval 15 – 20 mm) and four somewhat farther apart (interval 30 mm). Interruption of any of the light beams within a station initiated a 1 μs surge current on the signal line, which the interface unit used to initiate the signal to the computer. After a station had generated such a pulse, it could not send another for 10 s. This prevented the animal from triggering a single station more than once per pass. The light gate system had a resolution of 1 ms for the time difference between stations, which was considerably lower than the shortest period recorded between gates (77 ms).

Mice were placed at one end of the runway and were encouraged, by gently pinching their tails, or by clicking fingers or shaking keys behind them, to run along its length either toward or away from a darkened box situated at one end. Mice were run alternately in both directions starting from a random end, no more than five passes per day and never on

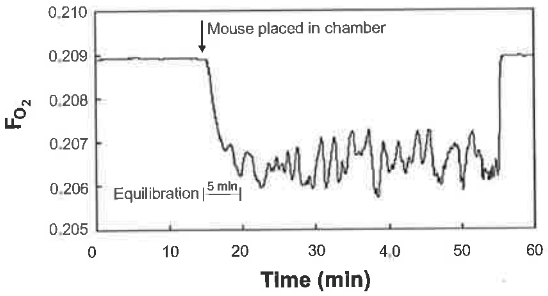

Figure 3.3. Example trace of typical burrowing trial (Female mouse, $M = 36.1$ g, excurrent airflow rate = 1.6 L min^{-1}). The mouse was placed in the chamber at the point indicated on the graph. It then explored the chamber and scratched at the soil for ~3 min, rested for ~1 min and burrowed for ~35 min. The washout after the mouse was placed in the chamber suggests an equilibration time of approximately 5 min.

consecutive days. For each day, the fastest speed across three gates (i.e. over 40 cm) was recorded, and MRS was calculated as the average of the three fastest speeds observed throughout the experiment.

Repeatability

Repeatability can be viewed as the proportion of the difference from the mean in one measure expected in another measure on the same individual and is calculated as the intraclass correlation coefficient, r_i (Dohm 2002). Calculation of r_i followed Zar (1999) and required multiple measurements of a trait for each individual. For BMR, repeatability was calculated using the two thermoneutral $\dot{V}_{O_2}$ measurements closest to T_{lc} that were separated by the largest time period (mean = 4.4 d) and obtained at T_a within 1 °C of one another. For determination of C_{wet} repeatability, $\dot{V}_{O_2}$s below T_{lc} were separated into two groups by date of measurement and C_{wet} was calculated for each group. Given that $\dot{V}_{O_2}$ of individual mice was never measured on consecutive days, individual measurements used for calculations of C_{wet} repeatability are separated by at least 2 d. Repeatability of T_b was calculated with the first and last T_b measurements, which were separated by an average of 5.4 d. $\dot{V}_{O_2\text{max}}$ repeatability was calculated using the maximum $\dot{V}_{O_2}$ observed on the first and last days of measurement, which were separated by 6 d. MRS repeatability was calculated using the fastest speeds recorded for each mouse on the first and last days of measurement, which were separated by 9 or 10 d.

Results

Thermoregulation and metabolism

The mean resting T_b of *N. alexis* (35.3 °C) is similar to that predicted on the basis of body mass (97% of predicted), but is more than 2 °C lower than the 37.7 – 38.3 °C normothermic range previously reported for this species (MacMillen and Lee 1970). Similarly, BMR is also less than that previously measured (0.75 mL O_2 min^{-1}: MacMillen and Lee 1970) and 90% of that predicted by allometry (Table 3.1, Figure 3.4). C_{wet} is similar to the allometric prediction (102%: Table 3.1, Figure 3.5) but is also less than previously reported (0.097 mL O_2 min^{-1} $°C^{-1}$: MacMillen and Lee 1970), as is T_{lc} (Table 3.1). $\dot{V}O_{2\max}$ was 75% of that predicted by allometry (Table 3.1, Figure 3.4) and represented a 6.4-fold elevation above BMR.

The factorial range in individual measurements of BMR (1.3-fold, Figure 3.4) was 16% of that observed between species (7.8-fold, Chapter 2). Individual BMR measurements ranged from 75 – 97% of that predicted by *M*. The factorial range of C_{wet} (1.2-fold) was also considerably less than that observed between species (5.2-fold, Figure 3.5). Individual measurements of C_{wet} ranged from 93 – 115% of that predicted by *M*. The factorial range of $\dot{V}O_{2\max}$ (1.5-fold, Figure 3.4) was similar to the factorial range observed in BMR, however, it encompassed almost half of the factorial range observed between species (3.1-fold, Figure 3.4). Individual $\dot{V}O_{2\max}$ measurements ranged from 61 – 93% of predicted.

Locomotion

$\dot{V}O_{2b}$ represented a 5.7-fold elevation above BMR and averaged 89% of $\dot{V}O_{2\max}$ (Table 3.1). Individual $\dot{V}O_{2b}$ values were 63 – 103% of measured $\dot{V}O_{2\max}$. NCOT_b was 5650-fold higher than NCOT_p, and NCOT_p was higher than that predicted by allometry (122%: Table 3.1). Individual measurements of NCOT_p ranged from 82 – 173% of that predicted by *M*. U_{ma} was 37% of MRS and 5528-fold higher than U_b (Table 3.1).

Table 3.1. Measured and predicted physiological variables for *Notomys alexis*

	This Study		Published		Allometric	
	Mean ± s.d.	n	Measured	%	Predicted	%
M	33.0 ± 3.6	11	32.3 ± 4.8 [a]	102%		
T_b	35.3 ± 0.6	11	37.7 – 38.3 [a]	93%	36.3 [e]	97%
T_{lc}	28.9 ± 2.3	11	34 [a]	85%		
C_{wet}	0.085 ± 0.07	11	0.097 [a]	87%	0.083 [f]	102%
BMR	0.65 ± 0.05	11	0.75 ± 0.14 [a]	87%	0.73 [g]	90%
$\dot{V}_{O_2 max}$	4.18 ± 0.57	11	3.48 [b]	120%	5.57 [g]	75%
$\dot{V}_{O_2 b}$	3.70 ± 0.61	6				
U_{ma}	0.68 ± 0.17	7	0.83 [c]	82%	1.19 [d]	57%
MRS	1.83 ± 0.36	11	3.64 ± 0.30 [d]	50%	3.89 [h]	47%
U_b	0.0074 ± 0.0008	6				
NCOT$_b$	7119 ± 883	6				
NCOT$_p$	1.26 ± 0.36	7	1.46 [c]		1.03 [i]	122%

Note to Table 3.1. Measured and predicted physiological variables presented as mean ± s.d or % of previously measured or predicted. n is sample size. References: [a] MacMillen and Lee (1970); [b] Cold-induced $\dot{V}_{O_2 max}$ (Hinds and Rice-Warner 1992); [c] Baudinette *et al.* (1976); [d] Garland *et al.* (1988); [e] Chapter 1; [f] Figure 3.5; [g] Figure 3.4; [h] Australian Muridae (Garland *et al.* 1988); [i] Full and Tullis (1990a).

T_b: Body temperature, °C
BMR: Basal metabolic rate, mL O_2 min^{-1}
$\dot{V}_{O_2 max}$: Maximum metabolic rate, mL O_2 min^{-1}
T_{lc}: Lower critical temperature, °C
C_{wet}: Wet thermal conductance, mL O_2 min^{-1} °C^{-1}
U_{ma}: Maximum aerobic speed, m s^{-1}
MRS: Maximum running speed, m s^{-1}
$\dot{V}_{O_2 b}$: Burrowing metabolic rate, mL O_2 min^{-1}
U_b: Burrowing rate, m min^{-1}
NCOT$_b$: Burrowing net cost of transport, J m^{-1}
NCOT$_p$: Pedestrian net cost of transport, J $^{\text{m-1}}$

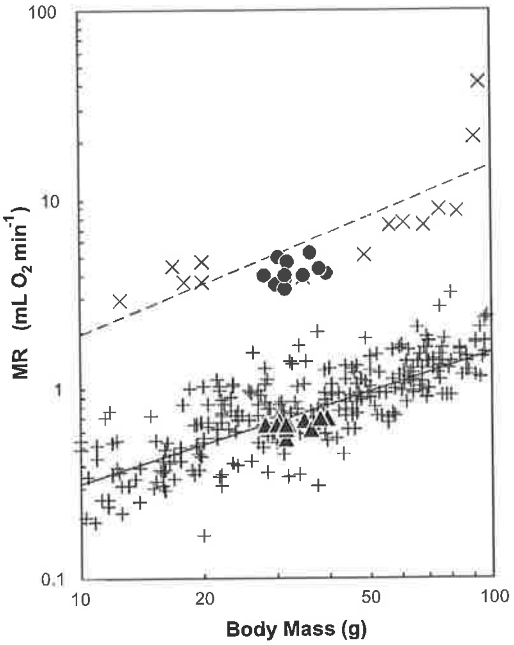

Figure 3.4. Relationship between body mass (M) and basal metabolic rate (BMR, ▲) and maximum aerobic metabolic rate (MMR, •) of individual hopping mice, *Notomys alexis*, compared to basal (+) and maximum aerobic (×) metabolic rate species means for a range of mammalian species (Appendix A; Seeherman *et al.* 1981; Taylor and Weibel 1981; Maloiy *et al.* 1982; Koteja 1987; Hinds and Rice-Warner 1992). Equations of the regression lines are as follows: BMR (solid line) = $0.0663\ M^{0.686}$, n = 571; MMR (broken line) = $0.256\ M^{0.881}$, n = 36. Only data within the range 10 g ≤ M ≤ 100 g are presented, but all available data were used to generate regressions.

Intraindividual repeatability and interindividual variation

Five variables were assessed for intraindividual repeatability (Table 3.2). BMR, $\dot{V}o_{2\max}$, MRS, and T_b were all significantly repeatable ($p \leq 0.03$, Table 3.2) over periods of at least two days. The coefficient of variation (CV) for hopping mouse BMR was within the range reported for birds (Burness *et al.* 1998), but less than half of that reported for domestic mice (Dohm *et al.* 2001) and less than a quarter of that observed between species within Mammalia or Muridae (Table 3.3). Intraspecific CV for C_{wet}, T_b, $\dot{V}o_{2\max}$, and NCOT$_b$ are around 30% of Mammalia and 36-57% of Muridae. U_{ma} and NCOT$_p$ intraspecific CVs were more variable (60 and 72% of the CVs for Mammalia and 49 and 59% of CVs for Muridae, Table 3.3).

None of the 11 variables measured was significantly correlated with M ($-0.54 \leq r \leq 0.56$, $0.11 \leq p \leq 0.99$). These 11 variables allowed for examination of a total of 55 intraspecific correlations. With α set at 0.05, 5% (or 2 - 3) of these correlations are expected to be significant based on chance alone. Instead, however, 9 correlations were found to be significant (Table 3.4, Figures 3.6 – 3.10). C_{wet} was significantly correlated with BMR, T_b, T_{lc} and U_{ma}. U_{ma} was also significantly correlated with NCOT$_p$ and T_b. T_b was significantly

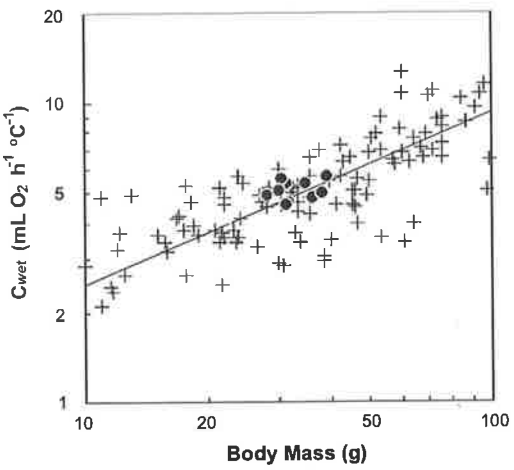

Figure 3.5. Relationship between body mass (M) and wet thermal conductance (C_{wet}, •) of individual hopping mice, *Notomys alexis*, compared to C_{wet} species means (+) for a range of mammalian species (McNab 1978; Aschoff 1981; McNab 1992a; McNab 1995; Baudinette *et al.* 2000; McNab 2000c; Arends and McNab 2001; McNab and Bonaccorso 2001; Lovegrove 2003). Equation of the regression line: $C_{wet} = 0.662\ M^{0.576}$, n = 235. Only data within the range 10 g ≤ M ≤ 100 g are presented, but all available data were used to generate regressions.

correlated with $NCOT_p$, U_b was significantly correlated with MRS, and T_{lc} was significantly correlated with $\dot{V}_{O_2b}$. The only variables not significantly correlated with at least one other were $\dot{V}_{O_2\max}$ and $NCOT_b$.

Discussion

Thermoregulation and metabolism

Hopping mice are largely unremarkable in terms of their thermoregulatory and metabolic physiology. Hopping mouse data sit well within the range observed for other species (Figures 3.4 and 3.5). Where allometric predictions are available, variables measured for hopping mice are quite similar to those predicted (Table 3.1), suggesting that measured data are reliable. However, the measurements obtained here disagree with those obtained by MacMillen and Lee (1970) that showed higher T_b, BMR, T_{lc}, and C_{wet} (Table 3.1). This difference can be attributed to their use of pooled data. For example, because T_{lc} for individuals ranges from 25.7 to 33.3 °C in the present study (Figure 3.11), calculation of BMR within a thermoneutral zone defined from pooled data includes some non-thermoneutral measurements, thus increasing the estimate of BMR to 0.72 mL O_2 min^{-1}, which is significantly higher than that estimated from individual data ($t_{37} = 3.6$, $p < 0.001$), but is more similar to that predicted by allometry (0.73 mL O_2 min^{-1}: Table 3.1) and to the 0.75 mL O_2 min^{-1} reported by MacMillen and Lee (1970). Given that BMR is usually calculated from

Table 3.2. Repeatability estimates for a selection of variables

	r_i	n	p
BMR	0.69	11	0.005
C_{wet}	0.27	10	0.20
Rank C_{wet}	0.68	10	0.008
T_b	0.55	11	0.03
$\dot{V}_{O_2\max}$	0.82	11	0.0003
MRS	0.78	11	0.0009

r_i is the intraclass correlation coefficient (calculated according to Zar 1999), n is sample size, p is significance
BMR: Basal metabolic rate, mL O_2 min^{-1}
C_{wet}: Wet thermal conductance, mL O_2 min^{-1} °C^{-1}
Rank C_{wet}: C_{wet} ranked from largest to smallest
T_b: Body temperature, °C
$\dot{V}_{O_2\max}$: Maximum metabolic rate, mL O_2 min^{-1}
MRS: Maximum running speed, m s^{-1}

pooled data, this finding has important implications, because allometric analyses of BMR therefore potentially contain a number of non-basal measurements.

$\dot{V}_{O_2\max}$ in the present study was also lower than that predicted by allometry (Table 3.1). However, U_{ma} was considerably lower than MRS (Table 3.1) and $\dot{V}_{O_2}$ clearly did not increase above U_{ma} (e.g. Figure 3.1). This suggests that the low $\dot{V}_{O_2\max}$ does not represent a failure to achieve maximal levels of metabolism. Overall, the congruence between measured and predicted values suggests that the metabolic and thermoregulatory data obtained in this study are reliable.

Does calculation from pooled data alter BMR allometry?

A great deal of effort has been invested in the measurement of BMR, with data presently available for over 600 species of mammal (Appendix A). Generally, BMR is determined by making measurements that satisfy strictly defined guidelines (e.g. McNab 1997) for multiple individuals over a range ambient temperatures (e.g. MacMillen and Lee 1970; Arends and McNab 2001). Such data allow for determination of the thermoneutral zone, and BMR is calculated as average $\dot{V}_{O_2}$ for multiple individuals within this temperature range. However, determination of BMR in this manner potentially includes non-thermoneutral $\dot{V}_{O_2}$s and may

Table 3.3. Coefficients of variation for interindividual (within *Notomys alexis*) and interspecific (within Mammalia and Muridae) measures of a selection of physiological variables

	Notomys alexis		Mammalia		Muridae	
	n	CV	n	CV	n	CV
M	11	11%				
T_b	11	1.7%	507	5.1%	130	3.0%
BMR	11	7.7%	573	35%	166	32%
$\dot{V}O_{2\max}$	11	14%	22	43%	7	34%
T_{lc}	11	8.0%				
C_{wet}	11	8.3%	235	30%	78	23%
U_{ma}	7	25%	22	42%	4	51%
MRS	11	20%				
$\dot{V}O_{2b}^*$	6	16%	7	42%		
U_b	6	11%				
NCOT_p	7	29%	33	40%	3	48%
NCOT_b^*	6	18%	4	60%		

Note to Table 3.3. n is sample size, CV is the coefficient of variation. For interspecific comparisons, CV is the standard deviation of residuals from a ln-ln allometric relationship between the variable and body mass (Garland 1984). The standard deviation of Log_{10}-Log_{10} residuals is converted to CV by multiplying by 2.3026 (Garland 1984). Interspecific CV for NCOT_b^* and $\dot{V}O_{2b}^*$ however, were calculated from mass-independent measures (both $\propto M^{0.67}$: Chapters 1 and 5, Vleck 1979). For interindividual data, CV is the standard deviation divided by the mean. Interspecific data were compiled from a range of published sources (Appendix A; McNab 1978; Vleck 1979; Aschoff 1981; Seeherman *et al.* 1981; Taylor and Weibel 1981; Maloiy *et al.* 1982; Du Toit *et al.* 1985; Koteja 1987; Garland *et al.* 1988; Lovegrove 1989; Hinds and Rice-Warner 1992; McNab 1992a; 1995; 2000c; Baudinette *et al.* 2000; Arends and McNab 2001; McNab and Bonaccorso 2001; Lovegrove 2003).

M: Body mass, g
T_b: Body temperature, °C
BMR: Basal metabolic rate, mL O_2 min^{-1}
$\dot{V}O_{2\max}$: Maximum metabolic rate, mL O_2 min^{-1}
T_{lc}: Lower critical temperature, °C
C_{wet}: Wet thermal conductance, mL O_2 min^{-1} $°\mathrm{C}^{-1}$
U_{ma}: Maximum aerobic speed, m s^{-1}
MRS: Maximum running speed, m s^{-1}
$\dot{V}O_{2b}^*$: Burrowing metabolic rate, mL O_2 $\mathrm{g}^{-0.67}$ min^{-1}
U_b: Burrowing rate, m min^{-1}
NCOT_b^*: Burrowing net cost of transport, J $\mathrm{g}^{-0.67}$ m^{-1}
NCOT_p: Pedestrian net cost of transport, J m^{-1}

Table 3.4: Correlation coefficients (italicised, above diagonal) and p-values (below diagonal) for a range of physiological variables. Values in bold are significant ($p < 0.05$)

	BMR	$\dot{V}_{O_2\max}$	C_{wet}	U_{ma}	MRS	T_b	T_{lc}	$\dot{V}_{O_2b}$	U_b	NCOT_b	NCOT_p
BMR		*0.09*	***0.80***	*0.67*	*-0.03*	*0.39*	*-0.54*	*-0.32*	*0.15*	*-0.33*	*-0.70*
$\dot{V}_{O_2\max}$	0.79		*-0.08*	*0.10*	*0.32*	*-0.11*	*-0.14*	*0.13*	*-0.29*	*0.51*	*0.08*
C_{wet}	**0.003**	0.82		***0.76***	*-0.55*	***0.65***	***-0.71***	*-0.77*	*-0.52*	*-0.15*	*-0.58*
U_{ma}	0.10	0.82	**0.048**		*-0.63*	***0.82***	*-0.36*	*-0.39*	*-0.10*	*0.01*	***-0.91***
MRS	0.94	0.33	0.08	0.13		*-0.43*	*0.59*	*0.80*	***0.85***	*-0.13*	*0.34*
T_b	0.24	0.75	**0.03**	**0.03**	0.19		*-0.08*	*-0.24*	*-0.20*	*-0.01*	***-0.77***
T_{lc}	0.09	0.69	**0.01**	0.43	0.06	0.83		***0.88***	*0.73*	*0.04*	*0.09*
$\dot{V}_{O_2b}$	0.53	0.81	0.07	0.51	0.06	0.65	**0.02**		*0.75*	*0.31*	*0.00*
U_b	0.78	0.58	0.29	0.87	**0.03**	0.70	0.10	0.08		*-0.32*	*-0.31*
NCOT_b	0.52	0.30	0.78	0.98	0.81	0.98	0.94	0.50	0.48		*0.34*
NCOT_p	0.08	0.87	0.17	**0.004**	0.46	**0.04**	0.85	1.00	0.61	0.58	

BMR: Basal metabolic rate, mL O_2 min^{-1}
$\dot{V}_{O_2\max}$: Maximum metabolic rate, mL O_2 min^{-1}
C_{wet}: Wet thermal conductance, mL O_2 min^{-1} °C^{-1}
U_{ma}: Maximum aerobic speed, m s^{-1}
MRS: Maximum running speed, m s^{-1}
T_b: Body temperature, °C
T_{lc}: Lower critical temperature, °C
$\dot{V}_{O_2b}$: Burrowing metabolic rate, mL O_2 min^{-1}
U_b: Burrowing rate, m min^{-1}
NCOT_b: Burrowing net cost of transport, J m^{-1}
NCOT_p: Pedestrian net cost of transport, J m^{-1}

therefore overestimate BMR, as is demonstrated here for hopping mice. To my knowledge, no other comparison of BMR calculated from pooled and individual data has been made so it is difficult to speculate on the generality of this finding. Nevertheless, the potential influence of this finding on the allometry of BMR can be inferred by examining the influence of M on T_{lc}. If we assume that the upper critical limit of the thermoneutral zone is independent of M, and that non-thermoneutral $\dot{V}_{O_2}$s are likely to be more common in BMR calculations for species with narrow thermoneutral zones, negative T_{lc} scaling (i.e. $b < 0$, where $T_{lc} \propto b \ln(M)$) suggests that BMRs are likely to be overestimated for small species, and that the BMR scaling exponent may therefore be underestimated. Alternatively, positive T_{lc} scaling ($b > 0$) suggests that BMRs are more likely to be overestimated for large species, and that the BMR scaling exponent may therefore be overestimated. In order to quantify the possible influence that

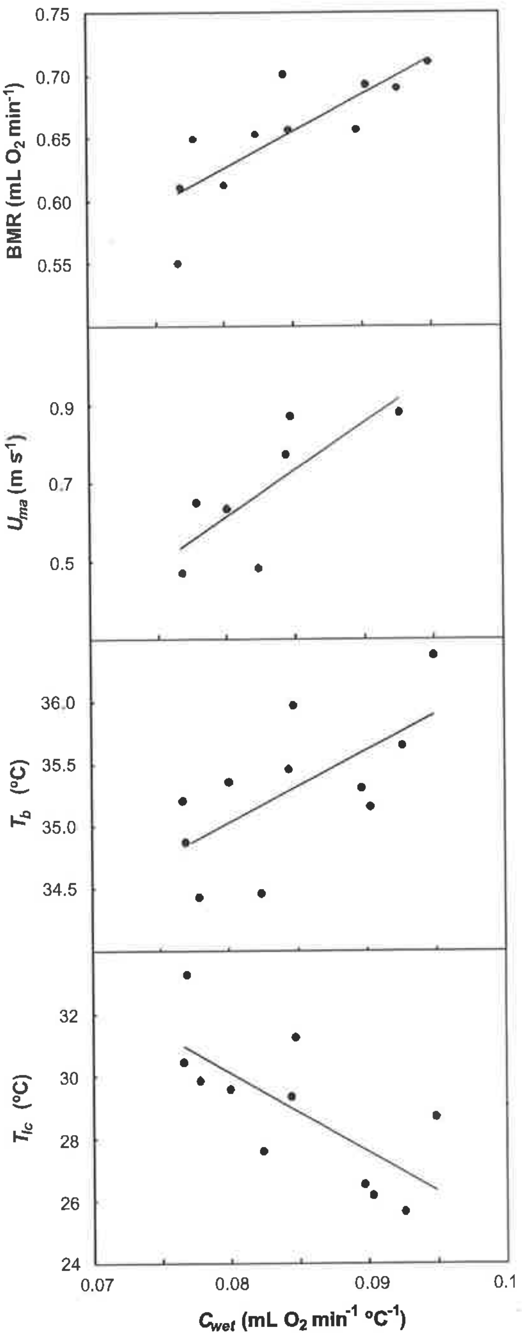

Figure 3.6. Correlations between wet thermal conductance (*C*wet) and basal metabolic rate (BMR, r = 0.8, n = 11, p = 0.003), maximum aerobic speed (U_{ma}, r = 0.76, n = 7, p = 0.048), body temperature (T_b, r = 0.65, n = 11, p = 0.03) and lower critical temperature of the thermoneutral zone (T_{lc}, r = -0.71, n = 11, p = 0.01)

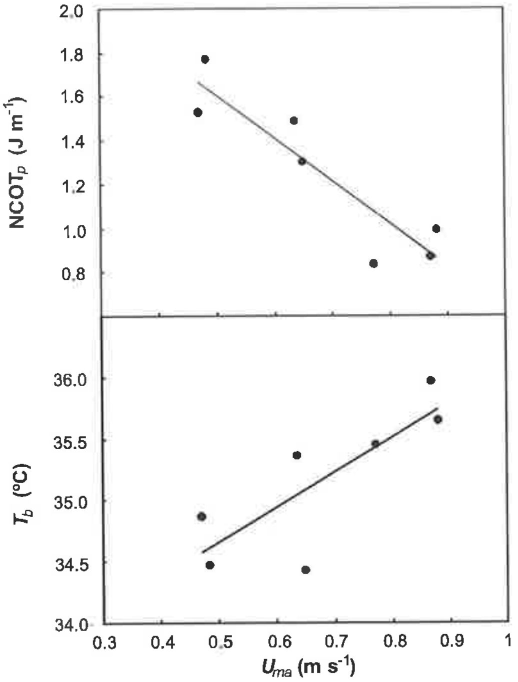

Figure 3.7. Correlations between maximum aerobic speed (U_{ma}) and net cost of pedestrian transport ($NCOT_p$, r = -0.91, n = 7, p = 0.004) and body temperature (T_b, r = 0.82, n = 7, p = 0.03)

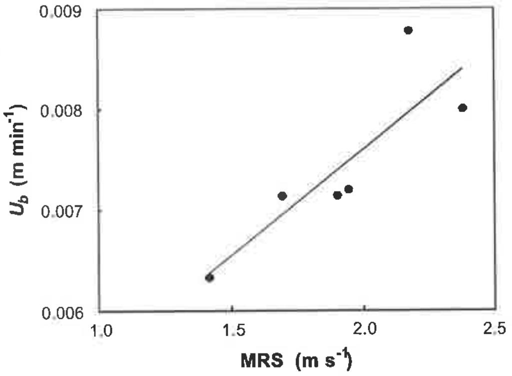

Figure 3.8. Correlation between maximum running speed (MRS) and burrowing speed (U_b, r = 0.85, n = 6, p = 0.03)

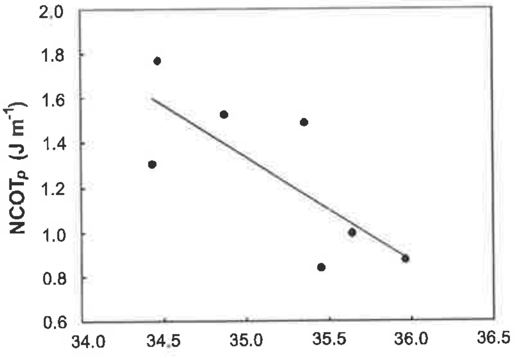

Figure 3.9. Correlation between body temperature (T_b) and net cost of pedestrian transport (NCOT$_p$, r = -0.77, n = 7, p = 0.04)

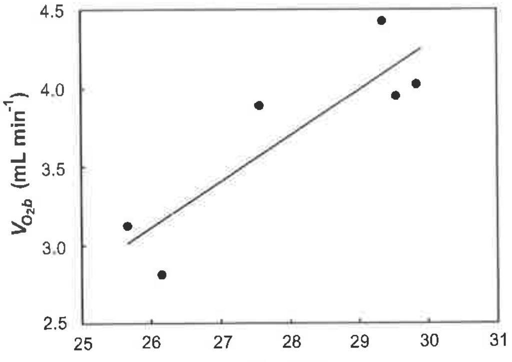

Figure 3.10. Correlation between lower critical temperature of the thermoneutral zone (T_{lc}) and burrowing metabolic rate ($\dot{V}_{O_2b}$, r = 0.88, n = 6, p = 0.02)

pooled data have on the estimation of the BMR scaling exponent it is therefore first necessary to examine the influence of M on T_{lc}. Assuming that animals are Newtonian objects, T_{lc} can be determined from BMR, C_{wet}, and T_b according to the equation:

$$T_{lc} = T_b - \frac{\text{BMR}}{C_{wet}}$$

This follows from the relationship between $\dot{V}_{O_2}$ and ambient temperature (T_a, °C) below T_{lc} ($\dot{V}_{O_2} = C_{wet}\,(T_b - T_a)$: Withers 1992) because the line relating $\dot{V}_{O_2}$ and ($T_b - T_a$) is equal to BMR where $T_a = T_{lc}$. For those mammals for which appropriate data are available (n = 215, sources provided with Figures 3.4 and 3.5), T_{lc} decreases with increasing M according to the equation: $T_{lc} = 31.4 - 1.28 \ln(M)$, which predicts a T_{lc} of 28.5 °C for a 10 g mammal and 16.7 °C for a 100 kg one. The thermoneutral zone is therefore likely to be wider for larger animals. This suggests that the lower end of the allometric regression relating BMR and M is potentially elevated by non-basal measurements and that the scaling exponent estimated from pooled data is artificially low. However, this suggestion is based on data for only a single species and examination of the differences between pooled and individual BMRs across a wide body mass range is clearly required to assess the generality of this conclusion. Where BMR is estimated as the mean minimal $\dot{V}_{O_2}$ obtained within the thermoneutral zone for each individual, on the other hand, BMR scaling is likely to be unaffected by pooling of data.

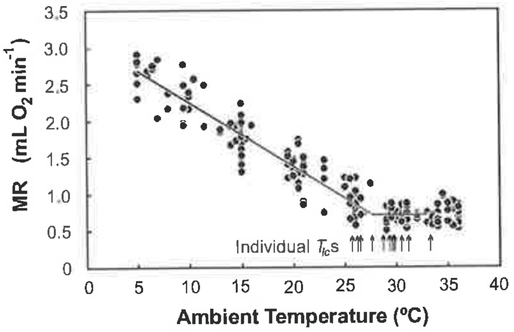

Figure 3.11. Effect of ambient temperature (T_a, °C) on the resting metabolic rate (MR, mL O_2 min^{-1}) of fasted *Notomys alexis*. Filled circles represent 193 measurements of 11 individuals. Below 27.6 °C, the relationship between MR and T_a is described by the equation (MR = 3.12 - 0.087 T_a). Between 27.6 and 33 °C, mean MR is 0.72 mL O_2 min^{-1}. The inflexion point of the relationship between T_a and MR for pooled data (27.6 °C) is similar to the mean individual thermoneutral lower critical temperature (T_{lc}, 28.9 °C, Table 3.1), however, the pooled relationship masks considerable individual variation (individual T_{lc}s are represented by arrows).

Locomotion

MRS was considerably lower than that predicted for Australian Muridae (Figure 3.12, Table 3.1) and previously measured for this species (Table 3.1). Although the maximum speeds observed in different portions of the runway were not significantly different, high speeds were observed most frequently in the middle of the 2.5 m runway (Figure 3.13), which may indicate that it was not long enough for animals to attain the maximum speeds of which they are capable. As such, MRS is unlikely to represent the maximum speed of which hopping mice are capable and may therefore not be strictly comparable with other measurements of MRS. Mean U_{ma} was also lower than predicted (Table 3.1), but the range of measurements overlap published values (Figure 3.12). Mean $NCOT_p$ was higher than predicted (Table 3.1), but the range of measurements overlapped the allometric prediction (Figure 3.14).

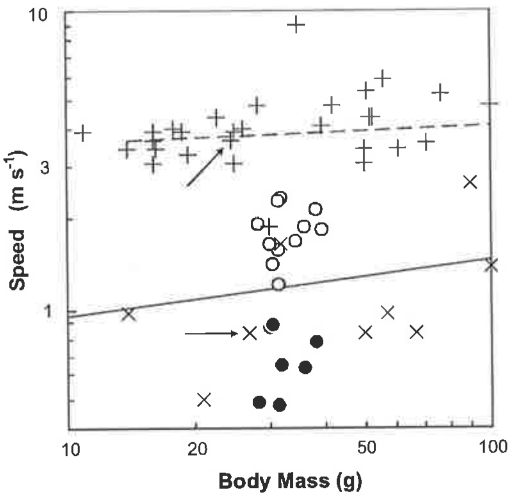

Figure 3.12. Relationship between body mass (*M*) and maximum running speed (MRS, ○) and maximum aerobic speed (U_{ma}, •) of individual hopping mice, *Notomys alexis*, compared to MRS (+) and U_{ma} (×) species means for a range of mammalian species (data from Garland *et al.* 1988). Regression lines are MRS for Australian Muridae (broken line: MRS = 3.22 $M^{0.054}$, n = 8) and U_{ma} for all mammals (solid line: $U_{ma} = 0.62\ M^{0.187}$, n = 41). Previous measurements of MRS and U_{ma} for *N. alexis* (Baudinette *et al.* 1976; Garland *et al.* 1988) are identified with arrows. Only data within the range 10 g ≤ *M* ≤ 100 g are presented, but data outside of this range were included in regression calculations.

Energetic costs and benefits of hopping and burrowing specialisation

Many of the convergent morphological specialisations observed among fully fossorial species are not shared with semi-fossorial species (e.g. structural developments of claws, forelimbs and pectoral girdle: Nevo 1979). As these specialisations are thought to increase burrowing efficiency, it might be reasonably expected that NCOT_b for semi-fossorial species would be higher than that of fossorial species. When normalised to burrow cross-sectional area, hopping mouse NCOT_b is 3 to 10-fold higher than that of other mammals burrowing through similar substrates (Table 3.5). This suggests either that semi-fossorial species burrow less efficiently than fossorial species or that the high NCOT_b of the hopping mice is an artefact. Hopping mice and semi-fossorial degus *Octodon degus* also have higher ratios of digging to basal metabolic rate than fossorial species (Table 3.5), which suggests that the high NCOT_b of hopping mice is real. It can therefore be tentatively concluded that the morphological specialisations observed in fossorial species are indeed adaptive and do act to reduce the energetic cost of burrowing. However, this conclusion is based on data for only a single semi-fossorial species and needs conformation with further study.

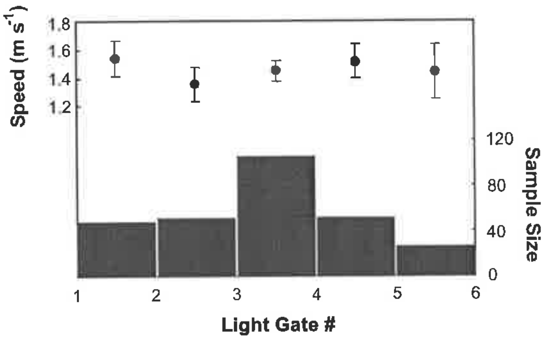

Figure 3.13. Mean maximum sprint speeds (± 95% CI) recorded between adjacent photoelectric light gates during 287 passes made by 11 mice along a 2.5 m runway (see methods). Mean sprint speeds observed between the gates are not significantly different (ANOVA $F_{4,282} = 1.4$, $p = 0.24$), but more high speeds were observed in the central portion of the runway.

To evaluate the possible benefits of specialisation for terrestrial rather than burrowing locomotion for hopping mice, it is informative to estimate the total cost of burrow construction and compare this with an estimate of the total energy used by a species of this size for terrestrial locomotion. Hopping mice commence burrow construction by excavating a sloping section to a depth of 70 to 150 cm (Lee *et al.* 1984). They then construct a system of horizontal tunnels and chambers from the bottom of the sloping tunnel. Finally, vertical shafts are excavated upward from the horizontal tunnels and the spoil generated by these diggings is used to backfill the sloping tunnels. A generalised system such as this may comprise five vertical tunnels and around 11 metres of horizontal tunnel and is usually occupied by five to eight adults and young of one or two litters (Lee *et al.* 1984). All adults assist in burrow construction and maintenance. For simplicity, it is assumed that each of five founding adults is responsible for construction of one sloping tunnel to a depth of 1.1 m, one vertical tunnel, and 2.2 m of horizontal tunnel. No data are available on the declination angle of the sloping tunnel, so data for a related species, *Notomys mitchellii*, are used (40°: Nowak 1999). The total cost of burrow construction can then be estimated using $NCOT_b$ together with estimates of burrow cross-sectional area (13 cm^2: Chapter 5), soil density (1.6 g cm^{-3}: Vleck 1979; Du Toit *et al.* 1985; Lovegrove 1989), and a model that incorporates $NCOT_b$

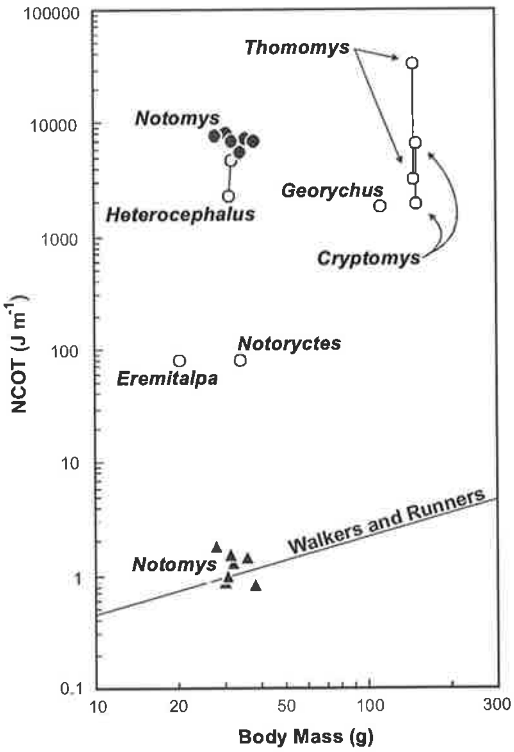

Figure 3.14. Relationship between body mass (M) and net cost of pedestrian (▲, NCOT$_p$) and burrowing (●, NCOT$_b$) transport for individual hopping mice, *Notomys alexis*. Unfilled symbols are published species mean NCOT$_b$ measurements for a variety of burrowing mammals (Vleck 1979; Du Toit *et al.* 1985; Lovegrove 1989; Seymour *et al.* 1998; Withers *et al.* 2000). Regression line is for NCOT$_p$ (Full *et al.* 1990).

together with the additional costs of working against distance and gravity to move spoil to the surface. The model is presented in Appendix C, together with an evaluation of some necessary assumptions. The model estimates a total construction cost of 55.5 kJ per mouse. Assuming that each mouse burrows at a speed similar to U_b while constructing this system, burrow construction will take around 11.2 h. Based on NCOT$_p$ and an allometric prediction of daily movement distances for a mammal of its body size (413 m: Garland 1983b), it is possible to estimate a daily terrestrial movement cost of 519 J, which is less than 1% of the estimated daily energy expenditure of this species (64 kJ: Nagy *et al.* 1999). Despite taking less than 12 h, burrow construction therefore requires a similar amount of energy to that expended in more than 100 days of terrestrial locomotion. Because of the apparently high cost of burrow construction relative to terrestrial locomotion, it therefore seems reasonable to ask why hopping mice are specialised for saltation rather than burrowing locomotion. The answer probably lies in the costs associated with such specialisation. Although the energetic costs of terrestrial locomotion of specialised burrowers (*Eremitalpa granti namibensis* and

Table 3.5. Net cost of transport by burrowing ($NCOT_b$) and metabolic rate (MR) measurements for a selection of mammalian fossorial and semi-fossorial species

	Mass (g)		$NCOT_b$ (J m^{-1})		MR (mL O_2 $g^{-0.67}$ h^{-1})			
	Digging	Basal		$g^{-0.67}$	Digging	Basal	Ratio	Reference
Heterocephalus glaber	31.5	32.0	2320	230	10.5	2.0	5.2	1, 2, 3
*Notomys alexis**	33.0	33.0	7119	684	21.3	3.8	5.7	This Study
Georychus capensis	113.0	195.0	1814	76	16.2	3.4	4.8	4, 5
Thomomys bottae	150.0	143.0	6430	224	21.4	4.3	5.0	6
Cryptomys damarensis	152.1	138.0	1968	68	15.9	2.9	5.5	3, 7, 8, 9
*Octodon degus**	203	193.0			38.6	5.0	7.7	10, 11, 12
Thomomys talpoides	300	106.8			25.7	6.2	4.1	13, 14, 15

Note to Table 3.5. Species labelled with * are semi-fossorial, the remainder are fossorial. All digging measurements were obtained in damp sand or sandy loam. $NCOT_b$ data are presented as whole animal measurements (J m^{-1}) and normalised to burrow cross-sectional area ($\propto M^{2/3}$: Chapter 5 and Vleck (1979)). To facilitate comparison between species of different size, digging and basal MR data are presented as mass independent (BMR $\propto M^{2/3}$: Chapters 1 and 2). Ratio refers to the ratio of digging metabolic rate to basal metabolic rate. Data were obtained from the following sources: (1) McNab (1966b), (2) Withers and Jarvis (1980), (3) Lovegrove (1989), (4) Du Toit *et al.* (1985), (5) Lovegrove (1987), (6) Vleck (1979), (7) Lovegrove (1986a), (8) Lovegrove (1988), (9) Bennett *et al.* (1992), (10) Bozinovic and Novoa (1997), (11) Ebensperger and Bozinovic (2000), (12) Arends and McNab (2001), (13) Bradley *et al.* (1974), (14) Gettinger (1975), (15) Andersen and Macmahon (1981)

Notoryctes caurinus) are similar to allometric predictions (Seymour *et al.* 1998; Withers *et al.* 2000), maximum running speeds of fossorial moles (*Talpa europaea* and *Scalopus aquaticus*) are only 20 – 30% of that predicted by body mass (Garland 1983a; Chappell 1989). Hopping mice forage in open areas in arid environments (Garland *et al.* 1988), so their capacity to escape predation is probably related to maximum running speed. Specialisation for burrowing is likely to occur at the expense of running speed, and is therefore likely to have a negative effect on overall fitness. For animals that can avoid predation through existence within a closed burrow system, however, the energetic advantages of burrowing specialisation are clear: a 65.2 g pocket gopher invests only 193 kJ in the construction of a labyrinth of feeding tunnels 52.5 m in length, whereas a 33.0 g hopping mouse constructing a system of similar length would expend 552 kJ (calculated using a modified version of the model described in Appendix C together with data from Vleck (1979; 1981)).

Intraindividual repeatability and interindividual variation

If a trait is to evolve under natural selection, it must be heritable, it must show stable interindividual variation that can be acted upon by selection, and it must influence the fitness of individuals. This study has demonstrated significantly repeatable interindividual variation in most measured traits. C_{wet} was the only trait that was not significantly repeatable because of a significant reduction in C_{wet} across the experimental period ($t_9 = 5.0$, $p = 0.001$). The intraclass rank correlation coefficient is significant, however ($r_i = 0.68$, $p = 0.008$). The significant repeatability of all traits for which it was assessed (Table 3.2) shows that interindividual variation is stable and suggests significant heritability. Overall, interindividual variation in the ten measured traits measured in this study is equivalent to 24 – 59% of that observed within the family Muridae and is 22 – 72% of that observed within Mammalia as a whole (Table 3.3). Variation within this single captive population therefore remains considerable despite laboratory rearing. Because all individuals were raised under similar conditions, this suggests a genetic component to variation. Overall, the general congruence between measured and predicted values (Table 3.1), high intraindividual repeatability (Table 3.2), and considerable interindividual variability (Table 3.3) suggests that the traits considered here could be influenced by selection. Variation between individuals therefore potentially has adaptive significance and examination of interindividual differences is appropriate.

BMR correlates

One of the aims of this study was to assess intraspecific correlated variation in BMR. Of the 10 variables measured, only C_{wet} was significantly correlated with BMR. This positive correlation suggests that BMR is influenced by heat loss: individuals with high C_{wet} appear to compensate for relatively poor insulation with relatively high rates of heat production. This result is in disagreement with the finding that BMR of sugar gliders, *Petaurus breviceps*, does not differ between normal and He-O_2 atmospheres, despite a significant increase in wet thermal conductance in He-O_2 (Holloway and Geiser 2001). Nevertheless, the suggestion that BMR is influenced by heat loss is supported by interspecific data: mass-independent C_{wet} is significantly positively correlated with mass-independent measures of both BMR and body surface area (Figure 3.15), despite the lack of a significant correlation between BMR and body surface area (Chapter 2).

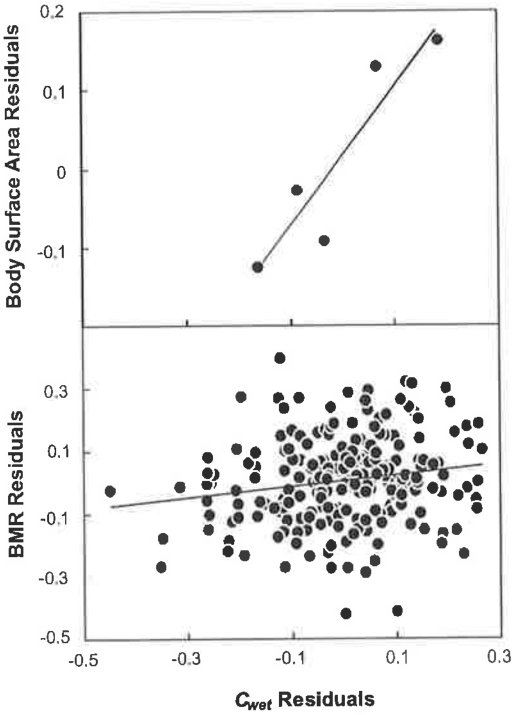

Figure 3.15. Interspecific mass-independent correlations between C_{wet} and body surface area and BMR. Residuals are calculated as the difference between $\log_{10}$(measured variable) and $\log_{10}$(predicted variable). Predictions are based on allometric relationships between the variable and body mass. BMR data provided in Appendix A, regression from Chapter 1. Body surface area data from Reynolds (1997). C_{wet} data from published sources (McNab 1978; Aschoff 1981; McNab 1995; Baudinette *et al.* 2000; McNab 2000c; Arends and McNab 2001; McNab and Bonaccorso 2001; Lovegrove 2003). Both correlations are significant (BMR: r = 0.17, n = 228, p = 0.01; Body surface area: r = 0.92, n = 5, p = 0.03).

It may also have been expected that BMR would be significantly correlated with $\dot{V}_{O_2\text{max}}$, because it is interspecifically for rodents (Hinds and Rice-Warner 1992) and intraspecifically for ground squirrels, *Spermophilus beldingi* (Chappell and Bachman 1995). Such a correlation is predicted by the aerobic capacity model for the evolution of endothermy (Bennett and Ruben 1979), which postulates that selection for increased aerobic capacity was important in the evolution of endothermy and that high levels of resting metabolism, and ultimately endothermy, arose as a correlated response. A key assumption of this model is a positive genetic correlation between $\dot{V}_{O_2\text{max}}$ and BMR (Hayes and Garland 1995), which has been tentatively demonstrated for house mice (Dohm *et al.* 2001). Phenotypic correlations between $\dot{V}_{O_2\text{max}}$ and BMR have been demonstrated for a number of taxa, but are by no means ubiquitous (reviewed by Hayes and Garland 1995), as is demonstrated here.

Interspecifically, BMR is positively correlated with T_b (Chapter 1), so a positive intraspecific correlation might also have reasonably been expected. The intraspecific correlation between BMR and T_b is positive but not significant (r = 0.39, p = 0.24) probably because of the relatively small sample size employed in this study. Similarly, the correlations between BMR and U_{ma} (r = 0.67), T_{lc} (r = -0.54), and NCOT$_p$ (r = -0.70) approach significance ($p \leq 0.1$, Table 3.4) and would therefore make appropriate traits for further studies of the adaptive significance of interindividual variation in BMR.

Intraspecific correlated variation

Although aimed primarily at the investigation of possible intraspecific correlations between BMR and 10 other physiological variables, the data obtained in this study also allow for the investigation of 45 additional correlations, eight of which are significant (Table 3.4). Although *post-hoc* explanations for these relationships are necessarily speculative and other explanations might be equally valid, an exploratory approach such as this is nevertheless useful because it can uncover relationships that are not anticipated and are deserving of further attention.

C_{wet} was significantly correlated with U_{ma}, T_b and T_{lc} (Figure 3.6). The positive correlation between C_{wet} and U_{ma} suggests that heat loss limits maximal limits of metabolism: aerobically fast mice have high C_{wet}. Presumably, the rate at which heat can be dissipated must be balanced with the rate at which it is produced and those individuals that are better able to dissipate heat are potentially able to operate at higher metabolic levels and therefore higher speeds. Although this hypothesis appears reasonable, the lack of a correlation between C_{wet} and $\dot{V}_{O_2\text{max}}$ fails to support it. The positive relationship between U_{ma} and C_{wet} might alternatively be mediated by the positive relationship between T_b and U_{ma}: given that heat loss is proportional to the difference between body and ambient temperature, high T_b could potentially facilitate dissipation of metabolic heat at a given ambient temperature, so high T_b might allow for high U_{ma}. However, the T_b range observed between mice (34.4 – 36.4 °C) only alters the temperature gradient between animal and environment by < 15%, and therefore appears insufficient to account for the 1.9-fold range observed in U_{ma} (0.47 – 0.88 m s^{-1}). U_{ma} is also significantly negatively correlated with NCOT$_p$ (Figure 3.7). This result, together with the lack of a significant correlation between $\dot{V}_{O_2\text{max}}$ and NCOT$_p$ (Table 3.4), suggests that hopping mice increase maximum aerobic speed by increasing locomotory efficiency rather than aerobic scope.

Individuals with high T_b have high C_{wet} (Figure 3.6), high U_{ma} (Figure 3.7), and low NCOT$_p$ (Figure 3.9). The correlation between C_{wet} and T_b is perhaps counterintuitive because one might reasonably expect that well-insulated individuals (low C_{wet}) would better retain heat and would therefore have higher T_b. However, BMR and T_b are positively correlated interspecifically (Chapter 1), and the intraspecific relationship is positive, but not significant

(Table 3.4). The positive relationship between C_{wet} and T_b may therefore represent a consequence of the positive relationships between C_{wet} and BMR and between BMR and T_b.

The correlations between T_b and both U_{ma} and NCOT$_p$ suggest that body temperature affects locomotory efficiency and that animals with high T_b convert metabolic to mechanical energy more efficiently than those with low T_b. This suggestion is supported by the observation that muscle function is generally impaired at low temperatures in both ectothermic vertebrates (Bennett 1985; Marsh and Bennett 1985) and mammals (Bennett 1985; Faulkner *et al.* 1990; De Ruiter and De Haan 2000). However, NCOT$_p$ and T_b are independent for blowflies (Berrigan and Lighton 1994), ants (Weier *et al.* 1995), toads (Walton *et al.* 1994) and lizards (Bennett and John-Alder 1984), but not ghost crabs (Weinstein and Full 1994). Similarly, NCOT$_b$ of Namib Desert golden moles (*Eremitalpa granti namibensis*) is independent of T_b, but NCOT$_p$ is lowest at high speeds, and warmer individuals attain the highest speeds (Seymour *et al.* 1998). Unfortunately, it is difficult to generalise from these findings, because the species for which NCOT$_p$ and T_b are independent are ectothermic, and the only mammal for which data are available is a poor thermoregulator with a low and labile T_b, and may therefore not accurately represent mammals in general. Nevertheless, it is possible that the negative correlation between T_b and NCOT$_p$ for hopping mice arises through a temperature effect on muscle function (i.e. low T_b individuals are further from the thermal optima for muscle function). The lack of a significant correlation between T_b and MRS in hopping mice (Table 3.4) and ground squirrels *Spermophilus tereticaudus* (Wooden and Walsberg 2004), suggests muscles are able to maintain contraction velocities and force production at low T_b *in situ*. This could potentially occur through increased fibre recruitment, which would increase the energetic cost of muscle contraction and also account for the negative correlation between T_b and NCOT$_p$, but a more comprehensive manipulative study of the effect of T_b on muscle function and cost of locomotion for mammals is required for a more definitive answer.

The positive correlation between T_{lc} and $\dot{V}_{O_2b}$ (Figure 3.10) may arise because all burrowing $\dot{V}_{O_2}$ trials were conducted at an ambient temperature of ca. 20 °C, which is below the measured T_{lc} of all individuals (Figure 3.11). Individuals with high T_{lc} were therefore further from thermoneutrality than those with low T_{lc} and, at rest, would require an increased rate of heat production to maintain T_b. The heat produced as a by-product of burrowing is therefore insufficient to meet the thermoregulatory requirements of the animals, which has also been demonstrated for naked mole-rats, *Heterocephalus glaber* (Lovegrove 1989). For hopping mice, an additional thermoregulatory cost is incurred during burrowing despite a 2.7-

fold increase in $\dot{V}_{O_2}$ above that observed at rest in air at 20 °C (1.38 mL O_2 min^{-1}: Figure 3.11). This additional thermoregulatory cost during burrowing might arise from a higher rate of heat loss by conduction to the soil, compared to the rate at rest in air.

The correlation between U_b and MRS (Figure 3.8) probably reflects the use of similar muscle groups for burrowing and running. Hopping mice are scratch-diggers: they burrow by loosening soil from the excavation face by scratching with the forelimbs. This soil is then pulled away from the excavation face with the forelimbs and kicked back toward the entrance with the hindlimbs. Burrowing activity was divided into three phases: scratching at the soil face, moving spoil along the tunnel to the entrance, and returning to the excavation face. Given that these activities necessarily occur discontinuously, it seems unlikely that animals were operating at a constant level. Blood lactate was not measured, but based on observations of burrowing it seems likely that scratching, which occurred in bursts punctuated by short rests, is at least partly anaerobic, whilst locomotion along the tunnel is entirely aerobic and probably somewhat below $\dot{V}_{O_2\text{max}}$. Because only short burrow segments were constructed and spoil could be kicked out of most of the tunnel without leaving the excavation face, U_b is therefore limited by the rate at which soil can be scratched away from the excavation face and kicked along the tunnel.

Acknowledgements

Russ Baudinette provided a high-speed treadmill, the raceway and photoelectric timers. Jayne Skinner and Steve Milne provided helpful advice regarding use of the photocell-timed raceway. Chris Leigh and Bill Breed allowed access to the mice and were exceedingly understanding throughout an early administrative hiccup. Jayne Skinner maintained the mice, and Belinda Waltman helped in her absence. Philip Matthews assisted with data collection throughout the early stages of this project. The University of Adelaide Animal Ethics Committee approved all experimental procedures.

4. The influence of foraging mode and arid adaptation on the basal metabolic rates of burrowing mammals

Abstract

Two competing but non-exclusive hypotheses to explain the reduced basal metabolic rate (BMR) of mammals that live and forage underground (fossorial species) are examined by comparing this group with burrowing mammals that forage on the surface (semi-fossorial species). These hypotheses suggest that the low BMR of fossorial species either compensates for the enormous energetic demands of subterranean foraging (the cost of burrowing hypothesis) or prevents overheating in closed burrow systems (the thermal stress hypothesis). As phylogenetically informed allometric analysis showed that arid burrowing mammals have a significantly lower BMR than mesic ones, fossorial and semi-fossorial species were compared within these groups. The BMRs of mesic fossorial and semi-fossorial mammals could not be reliably distinguished, nor could the BMRs of large (> 77 g) arid fossorial and semi-fossorial mammals. This finding favours the thermal stress hypothesis, as the groups appear to have similar BMRs despite differences in foraging costs. However, in support of the cost of burrowing hypothesis, small (< 77 g) arid fossorial mammals were found to have a significantly lower BMR than semi-fossorial mammals of similar size. Given the high mass-specific metabolic rates of small animals, they are expected to be under severe energy and water stress in arid environments. Under such conditions, the greatly reduced BMR of small fossorial species may compensate for the enormous energetic demands of subterranean foraging.

Introduction

Among those animals that seek subterranean refuge, two groups can be distinguished. Semi-fossorial animals (e.g. pouched mice *Saccostomus campestris*) forage on the surface and construct burrow refuges that may be used for caching food, reproduction, etc., whereas truly fossorial animals (e.g. pocket gophers *Thomomys bottae*) live and forage entirely beneath the surface (McNab 1979b; Nevo 1979). Generally, semi-fossorial species construct relatively short, structurally simple burrow systems whereas those excavated by fossorial animals are longer, more complex, and represent a much more substantial energetic investment (Vleck 1979; 1981).

Fossorial animals show a reduction in basal metabolic rate (BMR) below allometric predictions based on other mammals (McNab 1979b; Lovegrove 1986a; Bennett and Spinks 1995). The cost of burrowing hypothesis suggests that reduced BMR may compensate for the enormous energetic demands of subterranean foraging (Vleck 1979; 1981). The thermal stress hypothesis proposes that reduced BMR may minimise the chance of overheating in closed burrow systems where evaporative water loss and convective cooling are substantially reduced (McNab 1966b; 1979b).

While the cost of burrowing hypothesis remains largely unchallenged, much of the support for the thermal stress hypothesis is somewhat equivocal (e.g. Contreras 1986), and a reanalysis of McNab's (1966b) early data by Gettinger (1975) even provided an opposing interpretation. Gettinger's (1975) analysis indicated that fossorial animals have lower thermal conductance than is expected based on body mass. This supports the idea that prevention of hypothermia is more important than overheating.

Since these studies, a wealth of information on BMR for both fossorial and semi-fossorial species has accumulated, phylogenetically informed analyses have strengthened tests of adaptation (Harvey and Pagel 1991; Garland *et al.* 1993; 1999; Garland and Ives 2000) and many phylogenies of mammals have appeared, two of which are considered here (Novacek 1992; Madsen *et al.* 2001). This study uses this information to test the cost of burrowing and thermal stress hypotheses by allometrically comparing BMRs of fossorial and semi-fossorial burrowers. Additionally, distinction was made between animals from arid and mesic environments because arid adapted animals tend to have a lower metabolic rate than those from mesic environments (e.g. McNab 1979a; Maloiy *et al.* 1982; Lovegrove 1986b; Haim 1987; Downs and Perrin 1994; Seymour *et al.* 1998). This design accounts for a greater proportion of residual variation in BMR and facilitates comparison of fossorial and semi-fossorial species in an environment where differences relating to thermal stress and low foraging energy returns (both of which are expected to be exacerbated in arid environments) might be most prominent. Given that only fossorial mammals forage beneath the surface, if they have a lower BMR than semi-fossorial species, the cost of burrowing hypothesis would be supported. Alternatively, allometrically similar BMRs would support the thermal stress hypothesis, because the reduction in BMR can then be attributed to factors common to both groups, of which burrow construction and occupancy are immediately obvious.

Methods

Allometric relationships between BMR and body mass

Values for basal metabolic rate (BMR, mL O_2 min^{-1}) were sourced from the literature (Appendix D). Where multiple values were available for a species, the arithmetic mean was calculated. Values were accepted only if the animals were resting and conscious. Adult body mass was obtained from multiple published sources when body mass was not provided in a paper from which measurements were used. The data were disregarded if no body mass could be found in reputable literature. Log-transformed data were expressed in the form of least-squares regression of log-BMR on log-body mass. Felsenstein's (1985) phylogenetically independent contrasts were calculated using the PDTREE module of the PDAP suite of programs (Garland *et al.* 1993; 1999; Garland and Ives 2000). Phylogenetically informed regression slopes were calculated by producing a scatter plot of the standardised contrasts for log(BMR) and log(M) and computing a linear least-squares regression constrained to pass through the origin. A phylogenetically informed regression equation was then mapped back onto the original data by constraining a line with this slope to pass through the bivariate mean estimated by independent contrasts (e.g. Garland *et al.* 1993). Species were scored as fossorial or semi-fossorial according to descriptions of the main site of feeding in the reference from which BMR data were taken. If this source provided insufficient information for classification, further information was found in a general textbook on mammals (Nowak 1999). Classification of species as arid or mesic followed the same procedure, and was based on the original description of the species' habitat. Generally, species described in the literature as semi-arid were pooled with arid species, except where such a classification conflicted with other reports, in which case the most common classification was adopted.

Phylogenetic analysis of covariance

Inter-group comparisons of BMR were made using conventional and phylogenetic ANCOVA ($\alpha = 0.05$). Phylogenetic ANCOVA was undertaken using the PDTREE, PDSIMUL, PDANOVA and PDSINGLE modules of the PDAP suite of programs (Garland *et al.* 1993; 1999; Garland and Ives 2000). Phylogenetic ANCOVA was undertaken based on two phylogenies (Novacek 1992; Madsen *et al.* 2001). These trees differed topologically only

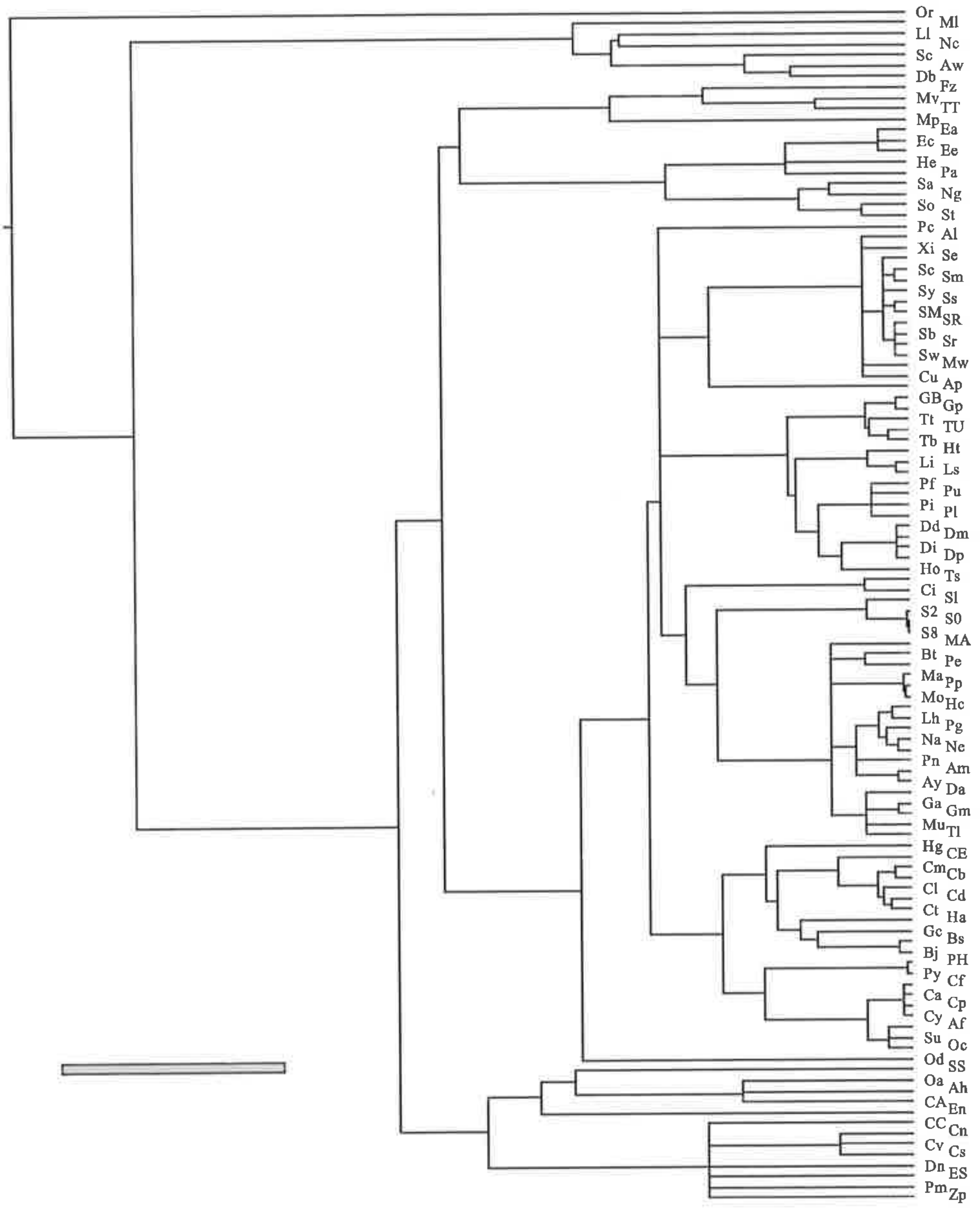

Figure 4.1. Hypothesised phylogeny based on Madsen *et al.* (2001) and other references (see Appendix E for details). Phylogeny based on a combination of molecular clock and fossil information. Branch lengths represent time since divergence, scale bar represents 50 MY, total tree height 200 MY. Two-letter codes denote tip species (see Appendix D).

in the relationships at family level and above. With respect to the species considered in this analysis, the major topological difference between the trees lies in the arrangement of Insectivora. Madsen *et al.* (2001) consider this order not to be monophyletic: Chrysochloridae and Tenrecidae lie within the Afrotheria clade whilst the remaining insectivores lie within the Laurasiatheria clade. With the exception of these differences, the phylogenies are identical. The tree based on most recent information is depicted in Figure 4.1. The inclusion of two phylogenies was intended to reduce the degree to which the study was affected by the uncertainty of phylogenetic hypotheses.

A gradual Brownian model of evolution, with limits, was used for all evolutionary simulations conducted for phylogenetic ANCOVA. Ten thousand simulations were used for each comparison and data were constrained using the 'throw out' algorithm, which restarts any simulation in which characters move outside specified limits. The minimum mass of simulated node and tip species was 1 g. This is similar to the minimum used in other studies, under the assumption that the smallest extant or extinct mammal probably weighed no less than 1 – 2 g (Garland *et al.* 1993). The maximum permitted mass was 100 kg. This is roughly twice the mass of the aardvark, *Orycteropus afer*, which is the largest burrowing mammal in the current data set. This mass range encompasses all extant burrowing mammals (Woolnough and Steele 2001). Minimum permitted BMR was 0.004 mL O_2 min^{-1}, which is one twentieth of that of *Eremitalpa granti namibensis*, which had the lowest BMR of the small mammals. Maximum BMR of simulated node and tip species was 205 mL O_2 min^{-1}, which again is roughly twice that of *O. afer*. The starting mean and variance of each evolutionary simulation was set to be the same as those for the tip species in the analysis (i.e. there was assumed to be no directional evolutionary trend in mass or BMR). The correlation between mass and BMR of the simulated data was also identical to that of the input data.

Comparison of groups with heterogenous regression slopes

Where ANOVA finds a significant interaction between a covariate and treatment effects (i.e. heterogenous regression slopes), analysis of adjustment treatment means using ANCOVA cannot be undertaken because the magnitude of the treatment effect will vary as a function of the covariate. However, application of the Johnson-Neyman technique allows determination of a 'region of non-significance' within which group elevations are not significantly different (Chapter 8). Where significantly heterogenous regression slopes were detected in this study, the Johnson-Neyman technique was applied at a significance level of $\alpha = 0.01$. Use of a low

Table 4.1. Regression equations and predicted basal metabolic rate (BMR, mL O_2 min^{-1}) values calculated using conventional or phylogenetically informed regression (PI, using phylogeny of Madsen *et al.* (2001)) for all burrowing mammals, or for those from arid or mesic environments. Regression equations are of the form BMR = a M^b, where M is body mass (g)

				Predicted BMR (mL O_2 min^{-1})			
Regression Method	Subset	a	b	10 g	100 g	1 kg	10 kg
Conventional	All	0.073	0.643	0.321	1.41	6.19	27.2
PI	All	0.048	0.698	0.241	1.20	6.00	29.9
Conventional	Arid*	0.067	0.647	0.296	1.31	5.82	25.8
PI	Arid*	0.036	0.738	0.197	1.08	5.91	32.2
Conventional	Mesic	0.112	0.586	0.433	1.67	6.42	24.7
PI	Mesic	0.098	0.605	0.394	1.59	6.39	25.7

* Excluding those species found to be different from the remainder by the Johnson-Neyman technique

significance level was intended to compensate for the lack of phylogenetic information incorporated in the Johnson-Neyman technique. This was considered appropriate because phylogenetically informed statistical methods typically have confidence intervals wider than those calculated using conventional statistical methods (Garland *et al.* 1999).

Results

Phylogenetically informed analyses using each of the phylogenetic hypotheses were generally in agreement and double-log least-squares regression exponents and coefficients for the two phylogenetic methods are remarkably similar, typically differing only in the 3rd or 4th decimal place. For this reason, only results of conventional and phylogenetically informed regressions arbitrarily based on Madsen *et al.* (2001) are presented (Table 4.1). Results of ANCOVA analyses are summarised in Table 4.2. All analyses detected a difference between arid and mesic species, so comparison of fossorial and semi-fossorial species was undertaken within these groups (Figures 4.2a and 4.2b). Both conventional and phylogenetic ANCOVA detected a difference between the slope of the double-log regressions for arid fossorial and arid semi-fossorial mammals (Table 4.2). However, the Johnson-Neyman technique showed that arid fossorial mammals with a mass less than 76.7 g have a BMR lower than arid semi-fossorial mammals, whilst those with a greater mass have a BMR statistically

Table 4.2. ANCOVA results for comparison of basal metabolic rate for fossorial/semi-fossorial mammals and arid/mesic using conventional or phylogenetically informed (PI: using phylogeny of Madsen *et al.* 2001) statistical methods.

Comparison				
Analysis Method	Subset	Source	F	p
Arid vs. Mesic				
Conventional	All	Among slopes	5.66	0.019
		Among groups	N/A	
PI	All	Among slopes	5.66	0.087
		Among groups	1.42	< 0.005
Fossorial vs. Semi-fossorial				
Conventional	All	Among slopes	0.178	0.67
		Among groups	0.13	0.72
PI	All	Among slopes	0.178	> 0.9
		Among groups	0.13	> 0.9
Conventional	Arid	Among slopes	10.1	0.003
		Among groups	N/A	
PI	Arid	Among slopes	10.1	< 0.025
		Among groups	N/A	
Conventional	Mesic	Among slopes	4.5	0.038
		Among groups	N/A	
PI	Mesic	Among slopes	4.5	> 0.1
		Among groups	0.253	> 0.75

indistinguishable from arid semi-fossorial species ($p = 0.01$). Three fossorial species (*Notoryctes caurinus*, *Heterocephalus glaber* and *Eremitalpa granti namibensis*) were therefore separated from the remaining arid burrowing species (Figure 4.2a). The allometric regression for arid burrowing species therefore includes both fossorial and semi-fossorial species, with only *N. caurinus*, *H. glaber* and *E. g. namibensis* excluded. Mesic fossorial and semi-fossorial species were found not to have significantly different regressions of log (BMR) on log (body mass) (Figure 4.2, Table 4.2).

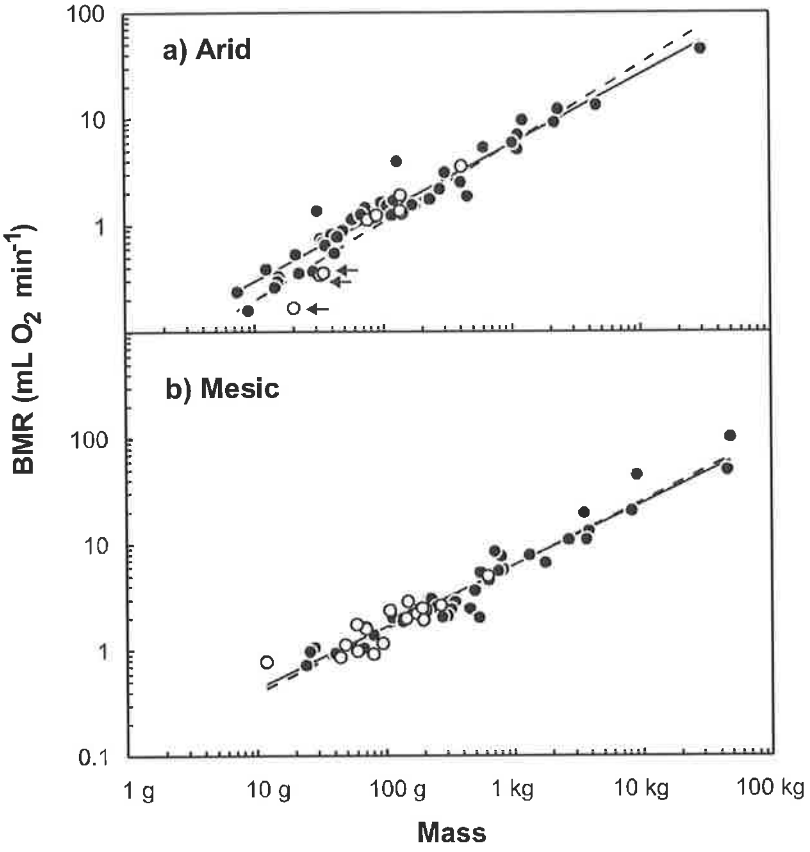

Figure 4.2. Relationship between body mass and basal metabolic rate for fossorial (○) and semi-fossorial (●) mammals from (a) arid and (b) mesic environments. Solid lines were calculated using conventional regression; broken lines were calculated using phylogenetically independent contrasts based on two phylogenetic hypotheses (Novacek 1992; Madsen *et al.* 2001) that were not visually distinguishable. Equations of the regression lines are in Table 4.1. The three arid species indicated with arrows have significantly different BMRs from the remaining arid burrowing species and were not included in the regressions for arid species (Johnson-Neyman technique, $p = 0.01$)

Discussion

Conventional or phylogenetically informed? On the choice of method

Although conventional and phylogenetically informed (PI) ANCOVA are generally in agreement (Table 4.2), the regression equations produced by the different statistical approaches can differ markedly, as is the case for the regressions for arid burrowing species in this study. At the lower end of the mass range of these animals (10 g), the PI regression BMR estimate is 67% of the conventional regression estimate, whilst at the upper end of the mass range (10 kg) the PI estimate is 125% of the conventional regression estimate (Table 4.1). It is important to note, however, that the PI method neither systematically increases nor decreases regression slopes (Chapter 7; Ricklefs and Starck 1996). In some cases, PI regressions differ little from the conventional alternative, as is evidenced by the almost indistinguishable PI and conventional regressions for mesic burrowing animals (Figure 4.2a). Despite this, results of conventional and phylogenetically informed ANCOVA and regression have been provided both to demonstrate the differences between the methods and to show that, in this case, interpretation is largely independent of the statistical method preferred.

Reduced BMR of fossorial mammals: Cost of burrowing or thermal stress?

The cost of burrowing hypothesis (Vleck 1979; 1981) proposes that fossorial mammals have a reduced BMR to compensate for the enormous energetic demands of subterranean foraging. Logical extension of this idea leads to the hypothesis that fossorial animals should have lower BMRs than semi-fossorial animals. However, this study has shown that, for mammals from mesic environments, fossorial and semi-fossorial species do not have significantly different BMRs (Tables 4.1 and 4.2).

A recognised alternative to the cost of burrowing hypothesis is the thermal stress hypothesis, which proposes that fossorial animals have a reduced BMR to prevent overheating in closed burrow systems where evaporative water loss and convective cooling are substantially reduced (McNab 1966b; 1979b). Although rejection of the cost of burrowing hypothesis does not provide unequivocal support for the thermal stress hypothesis, the latter does provide an alternative explanation that must be examined. However, the thermal stress hypothesis is also not entirely satisfactory, because it neglects the possibility of heat loss by conduction to the soil, which has been shown to be important in the thermoregulatory physiology of both arid and mesic species. For example, arid species such as the antelope ground squirrel, *Ammospermophilus leucurus*, may tolerate transient hyperthermia during bouts of surface activity and then dissipate excess heat upon return to their burrows (Chappell and Bartholomew 1981a,b). Similarly, the damp subterranean environment occupied by the star-nosed mole *Condylura cristata* (Hickman 1983) could present a significant thermoregulatory challenge to fossorial animals, many of which are poor thermoregulators with low and labile body temperatures (Bradley *et al.* 1974; Bradley and Yousef 1975; Withers 1978a; Withers and Jarvis 1980; Bennett *et al.* 1994; Seymour *et al.*

1998; Withers *et al.* 2000). However, the star–nosed mole is able to regulate its body temperature precisely at ambient temperatures between 0 and 30 °C (Campbell *et al.* 1999). Such precision is required because of the high rates of conductive heat loss, both to water during aquatic foraging bouts and to soil while inactive within its burrow. It therefore seems likely that burrowing species have access to microenvironments where heat can be offloaded to the soil, though this may not always be possible in the uppermost soil layers where temperatures can rise above the upper limits of thermoneutrality (e.g. Lovegrove and Knight-Eloff 1988). In such cases, deeper regions of the soil are often significantly cooler.

In support of the cost of burrowing hypothesis, the present study has also shown that three small arid fossorial species, the Namib Desert golden mole *E. g. namibensis*, the north-western marsupial mole *N. caurinus* and the naked mole rate *H. glaber*, do indeed have a significantly lower BMR than other arid burrowing species (Figure 4.2a). Given their small masses, these animals are expected to have high mass-specific metabolic rates and might therefore be expected to be under severe energy and water stress in arid environments. Consequently, their reduced BMR compensates for the enormous cost of burrowing relative to the meagre returns available in arid environments.

Adjustment of BMR as an adaptation to arid environments

A vast body of literature exists regarding reduction of field and basal metabolic rates as an adaptation to arid environments in mammals (e.g.McNab 1979a; Maloiy *et al.* 1982; Lovegrove 1986b; Haim 1987; Downs and Perrin 1994; Seymour *et al.* 1998). The present work, which compares over a hundred species that occupy similar niches and show several orders of magnitude variation in body mass, supports the conclusion that arid animals have a reduced BMR relative to their mesic counterparts. The strength of this conclusion is further enhanced by phylogenetically informed analyses and the inclusion of two phylogenetic tree topologies. Conventional and phylogenetic analyses have also recently provided strong support for a reduction in BMR of arid birds (Tieleman and Williams 2000). The low BMR of arid animals may be associated with increasing lifespan in an environment where reproduction is not necessarily an annual event (Haim 1987). However, few published studies support this hypothesis. Comparing strains of laboratory mice *Mus musculus*, Storer (1967) reported a positive correlation between BMR and longevity, whilst Konarzewski and Diamond (1995) found that longer-lived strains have lower BMRs than shorter-lived strains. Several studies have reported no significant relationship between residual variation in BMR and residual variation in longevity (Read and Harvey 1989; Harvey *et al.* 1991; Symonds 1999; Morand and Harvey 2000). Lifespan and BMR are significantly negatively correlated (Chapter 2), however, arid mammals were found to have a lifespan not significantly different from mesic species (ANCOVA $F_{1,197} = 0.2$, $p = 0.65$). Therefore, although mammals with low BMRs live longer than animals with high BMRs, arid adapted mammals live no longer than their mesic counterparts, suggesting that the reduced BMR of arid animals is unlikely to have arisen as an adaptation to increase lifespan.

An alternative hypothesis explaining the difference in BMR between arid and mesic mammals, and the one favoured here, is that the low BMR of arid animals may reduce food requirements and energy expenditure in environments where resources are sparse and widely distributed (Lovegrove 1986a). This hypothesis is supported by experiments in which laboratory mice selectively bred for low food intake rates show a reduction in BMR relative to those selected for high food intake rates (Selman *et al.* 2001a; 2001b).

Acknowledgements

Ted Garland Jr supplied the PDAP suite of programs and provided helpful advice regarding their use.

5. The allometry of burrow geometry

Abstract

The allometric relationship between body mass and burrow cross-sectional area for burrowing animals holds across greater than six orders of magnitude variation in body mass, and includes species separated by more than 500 million years of evolution from two phyla (Arthropoda and Chordata), seven classes (Arachnida, Insecta, Malacostraca, Osteichthyes, Amphibia, Reptilia, and Mammalia) and both terrestrial and marine habitats. Only birds, which are bipedal and construct relatively large burrows, and vermiform animals, which construct relatively narrow burrows, are separated from the remaining burrowing species. No difference is found between fossorial (burrowing animals that forage beneath the soil surface) and semi-fossorial (burrowing animals that forage terrestrially) mammals, suggesting that modification of burrow cross-sectional area to increase the net energy yield by burrowing would require maladaptive modification of the mammalian body plan. However, solitary fossorial mammals do construct significantly larger nest chambers than semi-fossorial and colonial fossorial mammals. These large nest chambers probably allow for the incorporation of large amounts of nest-lining material and therefore assist in maintaining body temperature by providing a better thermally insulated microenvironment. This offsets the thermoregulatory problems faced by these animals, which are characterised by low, labile body temperatures and poor thermoregulatory ability. Colonial fossorial mammals, on the other hand, construct nest chambers that are the same relative size as those constructed by semi-fossorial mammals and probably maintain homeothermy by huddling with endothermic nest-mates.

Introduction

Burrowing animals usually show morphological and physiological adaptations for subterranean life, with strongly convergent traits often evolving repeatedly in separate lineages. For example, fossorial mammals (burrowing subterranean foragers) show structural reductions of limbs, tails, eyes, and external ears, together with structural developments of incisors, forelimbs, pectoral girdle, claws, sense organs, and pineal gland that complement each other to optimise burrowing capacities and efficiency (Nevo 1979). Burrowing reptiles typically show varying degrees of limb reduction and body elongation, together with cranial consolidation, size reduction and limited skull kinesis (Withers 1981; Andrews *et al.* 1987;

Lee 1998). Given the extent of these modifications, it seems reasonable to predict that selection would act to reduce burrow cross-sectional area, which is directly proportional to the cost of burrow construction (Vleck 1979). Such selective pressure is likely to be strongest for fossorial animals, because any reduction in burrowing cost increases the net energy yield from a given section of burrow. Additionally, subterranean resources are not uniformly distributed either vertically or horizontally (Andersen 1982; Jarvis *et al.* 1998). Vertically, subterranean resources often show a peak value at some depth below the surface, so the net energy yield by burrowing can be further increased by situating a burrow as near as possible to the zone of maximum resource density and minimising burrow cross-sectional area (Andersen 1982). Horizontally, for food items that show a clumped distribution (e.g. geophytes: Jarvis *et al.* 1998), construction of a narrow burrow also increases the probability of encountering consumable items with no increase in foraging costs, because a narrow burrow is longer than a wide burrow of the same volume and energetic cost.

Burrow systems constructed by endothermic homeotherms also often include a nest chamber that provides substantial thermoregulatory energy savings to the occupant (Casey *et al.* 1979) through inclusion of insulative nesting material (e.g. Begall and Gallardo 2000; Scharfe *et al.* 2001). Given that many fossorial animals are poor thermoregulators relative to semi-fossorial (burrowing terrestrial foragers) and other mammals (Bradley *et al.* 1974; Bradley and Yousef 1975; Withers 1978a; Withers and Jarvis 1980; Bennett *et al.* 1994; Marhold and Nagel 1995; Seymour *et al.* 1998; Withers *et al.* 2000), it can be hypothesised that fossorial mammals should require a better insulated nest than semi-fossorial ones.

In this study, the extent to which selection has influenced burrow cross-sectional area and nest chamber volume are evaluated by comparing the structures constructed by fossorial animals and semi-fossorial animals. This comparison is made according to allometric principles, which account for the effect of body mass. To date, such a comparison has not been attempted.

Methods

Values for burrow cross-sectional area (A_b, cm^2), nest chamber volume (V_n, cm^3) and body mass (M, g) were calculated from measurements sourced from the literature (Appendix F). Where multiple values were available, the arithmetic mean was calculated. Values were accepted only if obtained by measurement, rather than visual estimate. Where body mass was not provided in a paper from which measurements were taken, an appropriate mass was obtained from multiple published sources. If adult body mass could not be found in established literature, the data were disregarded. Only species that construct their own burrows were included. Species were classified into the following groups: Colonial fossorial mammals (colonial species that construct burrows that are used for subterranean foraging), solitary fossorial mammals (solitary species that construct burrows that are used for subterranean foraging), semi-fossorial mammals (mammals that construct burrow refuges, but forage above ground), birds, reptiles, scorpions and vermiform animals (which include earthworms and a marine isopod *Natatolana borealis*). No coherent groups including three or more species and spanning a mass range greater than one order of magnitude were obvious within the remaining species (mole-crickets, terrestrial isopods, spiders, frogs, fish, crabs, and lobsters), so they were set aside in two groups termed 'other vertebrates' and 'other invertebrates'.

Log-transformed data were expressed in the form of least-squares regression of variable on body mass. This allowed calculation of an allometric equation of the form $y = a M^{b}$, where y is the variable of interest, a is the allometric coefficient, M is body mass (g), and b is the allometric exponent. Inter-group comparisons were made with ANCOVA; significantly different pairs were identified using mass-independent data (mass-independent $y' = y M^{-b}$) and the Tukey-Kramer HSD test. For all tests α was set at 0.05.

Results

Burrow cross-sectional area

Measurements of burrow dimensions for 96 species spanning six orders of magnitude variation in body mass, and including species from three phyla (Annelida, Arthropoda, and Chordata), nine classes (Arachnida, Insecta, Oligochaeta, Malacostraca, Osteichthyes, Amphibia, Reptilia, Aves, and Mammalia) and both terrestrial and marine habitats are presented in Appendix F. The regressions of burrow area (A_b, cm^2) on body mass (M, g) show no significant allometric exponent heterogeneity (ANOVA $F_{8,74} = 0.90$, $p = 0.52$; common exponent = 0.63 ± 0.02 (SE), exponent 95% CI: 0.59 – 0.68) and significant differences in allometric coefficient (ANCOVA $F_{8,84} = 6.6$, $p < 0.001$). Birds construct significantly larger burrows than other species and vermiform animals construct significantly

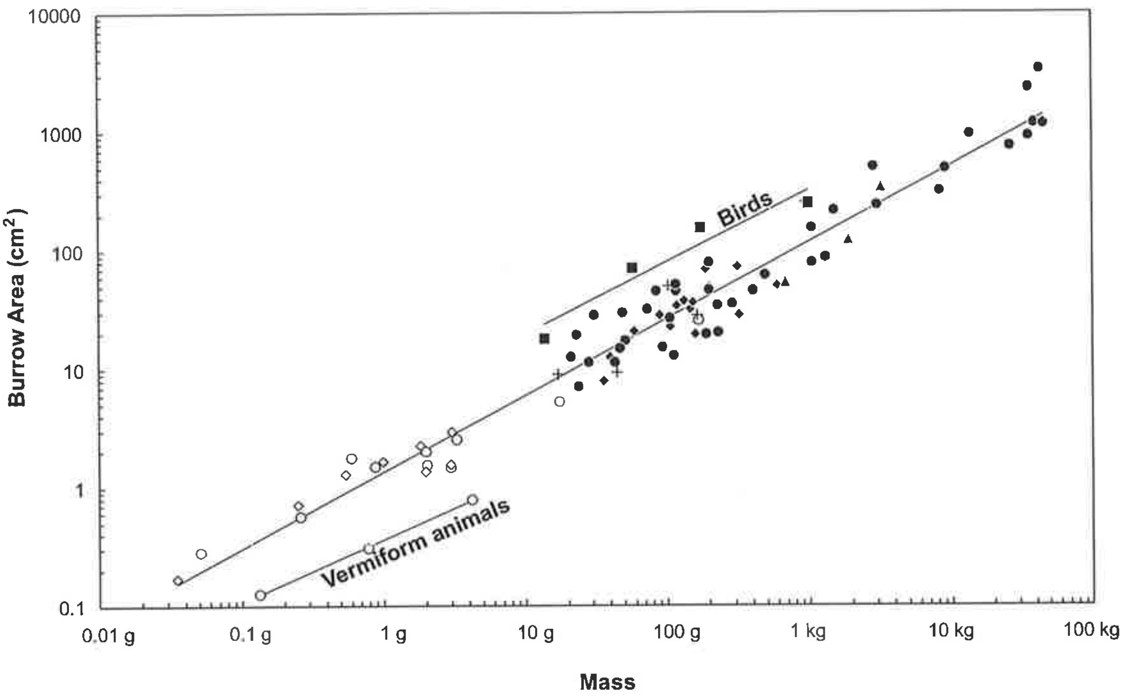

Figure 5.1. Relationship between burrow cross-sectional area (A_b) and body mass (M, g) for a variety of burrowing animals: fossorial mammals (◆), semi-fossorial mammals (●), birds (■), reptiles (▲), scorpions (◇), other vertebrates (+, see text for details), and other invertebrates (○, see text for details). Three statistically homogeneous groups were identified: birds, pooled (includes mammals, reptiles, frogs, fish, spiders, scorpions, mole crickets, a marine crab, and a terrestrial isopod), and vermiform animals (includes earthworms and a marine isopod). Birds: $A_b = 4.85\ M^{0.61}$, $r^2 = 0.93$; Pooled: $A_b = 1.34\ M^{0.65}$, $r^2 = 0.95$; Vermiforms: $A_b = 0.36\ M^{0.53}$, $r^2 = 0.999$.

smaller burrows (Tukey-Kramer HSD test of log-transformed mass independent burrow area A_b', cm^2 g$^{-0.63}$). The remaining groups (all mammal groups, other vertebrates, and non-vermiform invertebrates) cannot be distinguished and are combined into a group termed 'pooled' (Figure 5.1).

Nest chamber volume

Due to small sample sizes in most groups, nest chamber volumes can only be compared for birds, solitary fossorial mammals, colonial fossorial mammals and semi-fossorial mammals (Figure 5.2). These groups show no significant allometric exponent heterogeneity (ANOVA $F_{3,25} = 0.52$, $p = 0.74$; common exponent = 0.75 ± 0.06, exponent 95% CI: 0.63 – 0.87) and

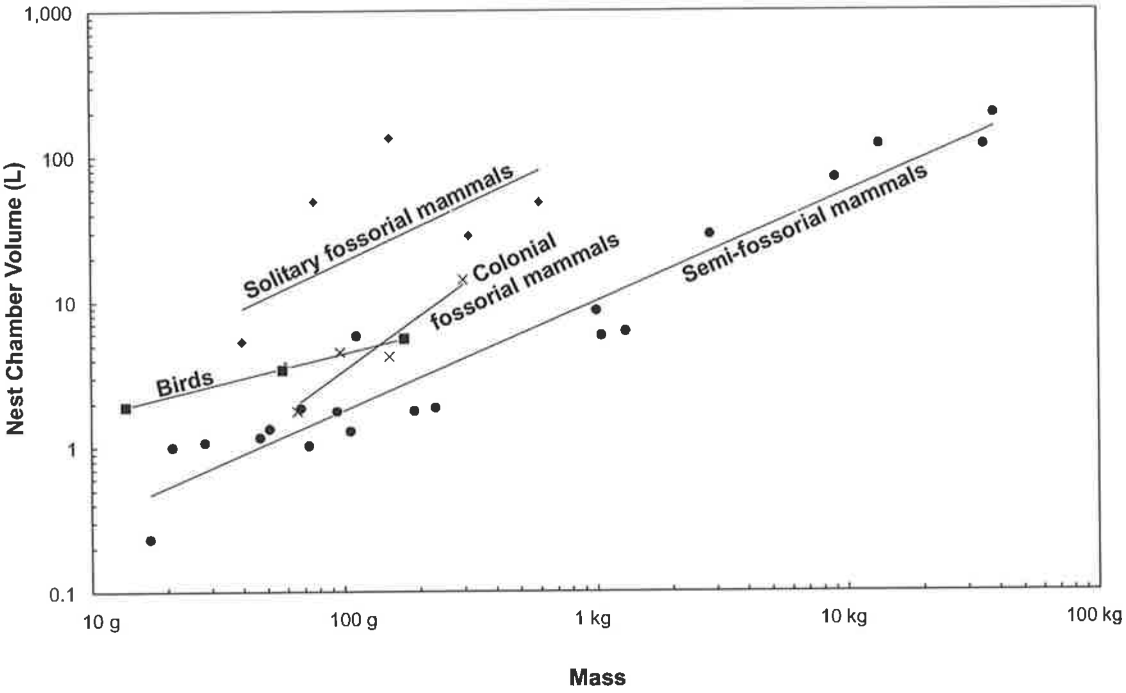

Figure 5.2. Relationship between nest chamber volume (V_n) and body mass (M, g) for a variety of burrowing animals: solitary fossorial mammals (◆), colonial fossorial mammals (×), semi-fossorial mammals (●), and birds (■). Colonial fossorial mammals: $V_n = 0.011\ M^{1.25}$, $r^2 = 0.90$; solitary fossorial mammals: $V_n = 0.46\ M^{0.80}$, $r^2 = 0.36$; semi-fossorial mammals: $V_n = 0.056\ M^{0.75}$, $r^2 = 0.93$; birds: $V_n = 0.63M^{0.42}$ $r^2 = 0.999$.

significant differences in allometric coefficient (ANCOVA $F_{3,30} = 28$, $p < 0.001$). A Tukey-Kramer HSD test of log-transformed mass independent nest chamber volume (V_n', L $g^{-0.75}$) shows that solitary fossorial animals construct nest chambers significantly larger than other animals. Colonial fossorial animals construct nest chambers that are not significantly different in size to those constructed by semi-fossorial animals. The nest chambers of birds are significantly larger than those constructed by semi-fossorial animals, but not significantly different in size to those constructed by colonial fossorial animals. Thus the ranking is:

solitary fossorial > birds^{a} > colonial fossorial^{a,b} > semi-fossorial^{b}

where groups with the same superscript characters cannot be statistically distinguished on the basis of nest chamber volume.

Discussion

Burrow cross-sectional area

The allometric relationship between burrow cross-sectional area and body mass is most prominently influenced by body mass and burrowing method. Ecological (foraging method) and phylogenetic influences are not evident, because fossorial and semi-fossorial mammals cannot be statistically distinguished, and mammals cannot be distinguished from a wide variety of other burrowing species (representing Arachnida, Insecta, Malacostraca, Osteichthyes, Amphibia, and Reptilia). It therefore seems that any advantages that could be conferred by a reduction in burrow cross-sectional area are outweighed by concomitant disadvantages arising from the morphological specialisations necessary for such a reduction. Burrowing requires the application of large forces to the substrate, which are associated with bulky muscles that insert far from joints, robust pelvic and pectoral girdles, heavy skulls, and strong scraping limbs or incisors (depending on digging method) (Nevo 1979; Hildebrand 1988). Any reduction in burrow area is likely to require reduction in these relatively bulky morphological components of the body, thereby reducing burrowing efficiency and counteracting any gains associated with a reduction in burrow area. Additionally, minimum burrow area may also be limited by the need to pass by other individuals in species that nest colonially and burrow in digging chains (e.g. *Octodon degus*: Ebensperger and Bozinovic 2000) or by the need to turn around in a burrow. If we assume that an animal turning back on itself within a confined space will adopt a roughly sperical shape, it is perhaps informative that the relationship between body mass and burrow cross-sectional area for pooled data is remarkably similar to that between the area of a plane through the centre of a sphere and its volume ($A = 1.21\ V^{2/3}$). Assuming a reasonable average density for an animal (1.075 g cm^{-3}: Withers 1992), the regressions cross at a mass of 2126 g and, within the range of animal masses considered here (35 mg – 45 kg), predicted burrow area is 124% to 94% of that predicted for a sphere. This suggests that burrow systems allow sufficient space for animals to turn around in tunnels, which may limit the extent to which burrow area can be reduced.

Although it might reasonably be expected that groups of related species descended from a common ancestor would conform to a single relationship between burrow radius and body mass, it is not immediately apparent why such a relationship would hold for species with such diverse body plans as those in the pooled group of this study. However, this common scaling pattern can be explained according to simple geometric principles. The basic derivation assumes that all animals have a similar body shape and predicts that burrow area should be proportional to $M^{2/3}$ (Vleck 1979), but some animals might, *a priori*, be expected not to conform to the pattern because they are not similarly shaped. Tortoises, for example, might be expected to have a larger burrow cross-section, given that they are somewhat more globular than the average mammal. In fact, the burrow size of the gopher tortoise *Gopherus polyphemus* is 140% of predicted, but is within the spread of data for mammals and other burrowing animals (Figure 5.1). Similarly, iguanas (*Iguana iguana*) are somewhat more elongate than the average mammal, and this is reflected in the relatively small burrow radius (71% of predicted), which is also within the spread of data for mammals and other animals. Snakes, however, are considerably more elongate than most other animals, but in this case, the method of burrow construction obscures the effect of body form on burrow size. Pine snakes burrow by pushing forward with the snout and head, crooking the neck, capturing sand in the crook, and bringing sand out to deposit it on a dump pile (Burger and Zappalorti 1991). Burrows therefore need to be somewhat wider than the animal in order to accommodate these movements.

The burrowing style of pine snakes contrasts with that of amphisbaenians, which burrow either by twisting and rotating the head to shave particles off the tunnel end and compact them into the tunnel wall, or by forcing the head into the soil to lengthen the tunnel and rotating the head to widen the tunnel (Gans 1969; 1974). Amphisbaenian burrows therefore approximate body dimensions, suggesting that they would fit within the vermiform group, although data on burrow dimensions are lacking. Other species that are expected to belong to this group include caecilians and uropeltid snakes, all of which construct burrows by moving through the substrate without producing an excavation face and without carrying spoil from the burrow (Gaymer 1971; Gans 1973; Gans *et al.* 1978). Species in the pooled group, on the other hand, burrow by scraping soil from the excavation face using their appendages, head, or teeth. Soil thus scraped may be pushed or carried from the burrow and either deposited on the surface (pouched mice, scorpions), used to backfill existing tunnels (e.g. gophers, mole rats) or compressed into the walls of the burrow (e.g. moles, mole crickets). Birds construct burrows that are significantly larger than those constructed by other animals. European bee-eaters (*Merops apiaster*) burrow by loosening soil with their beaks and kicking it backward with their feet (White *et al.* 1978). Burrow cross-sectional area is therefore strongly influenced by the height of the burrower because the animal must be able to stand so that spoil can be removed. Given that birds are likely to be taller than most other burrowing species of a similar body mass, bird burrows are relatively large to allow for passage of the occupant.

Nest chamber volume

An unexpected finding of this study is that solitary fossorial mammals construct subterranean nest chambers that are significantly larger than those of colonial fossorial or semi-fossorial mammals (Figure 5.2), despite statistically similar burrow cross-sectional areas. Both the solitary fossorial and semi-fossorial groups include representatives of Insectivora and Rodentia, reducing the likelihood that the large nest chamber of fossorial mammals is associated with phylogenetic differences between solitary fossorial and semi-fossorial groups. Potentially, the larger chamber constructed by solitary fossorial mammals could allow the incorporation of more nesting material and produce a nest with thicker walls and better thermal insulative properties then those of semi-fossorial mammals (Redman *et al.* 1999). For solitary fossorial animals, a large nest chamber is important from a thermoregulatory viewpoint, because many species have low, labile body temperatures (Bradley *et al.* 1974; Bradley and Yousef 1975; Withers 1978a). However, colonial fossorial mammals (*Cryptomys*, Bathyergidae) are also poor thermoregulators (Bennett *et al.* 1994; Marhold and Nagel 1995), but construct nest chambers that are not significantly larger than semi-fossorial mammals. In their case, thermoregulation may be improved by huddling with colony mates (Withers and Jarvis 1980; Yahav and Buffenstein 1991). Such behaviour provides both energetic benefits and increases the precision of homeothermy, thereby permitting smaller, less energetically costly nest chambers. Because ecological constraints in arid habitats are thought to have promoted the evolution of eusociality within the African mole-rats (Faulkes *et al.* 1997; Jarvis *et al.* 1998; Spinks and Plagányi 1999; Spinks *et al.* 2000), communal nesting may represent an adaptation to aridity that allows for energy savings both during and following nest chamber construction.

6. Requirements for estimation of the ‘true’ allometric exponent relating mammalian basal metabolic rate and body mass

Abstract

How many species covering what range of body masses are required to arrive at a reasonable estimate of the relationship between mammalian basal metabolic rate (BMR) and body mass (*M*)? The question could potentially be resolved if truly basal measurements from all 4600 extant species were available, but this is unrealistic. 4600 artificial species are therefore generated based on the variation in BMR and *M* observed in extant mammals and randomly selected subsets of the artificial species are examined to determine if calculation of a single ‘true’ allometric scaling exponent is currently possible. This analysis shows that 75 species spanning five orders of magnitude variation in body mass is sufficient to accurately determine the relationship between BMR and *M*.

Introduction

Allometry is a technique used to describe the effect of body mass on biological variables, which can often be described by a power equation of the form $y = a M^b$ where y is the variable of interest, a is the allometric coefficient, *M* is body mass, and b is the allometric or scaling exponent (e.g. McMahon and Bonner 1983; Peters 1983; Calder 1984; Schmidt-Nielsen 1984). When both variables are log-transformed, the relationship becomes a straight line of the form: $\log(y) = \log(a) + b \log(M)$. Perhaps one of the most frequently investigated relationships is that between *M* and basal metabolic rate (BMR, the rate at which an animal produces heat when postabsorptive and at rest, usually measured via indirect calorimetry as mL O_2 h^{-1}). Given that heat loss occurs predominantly through the surface of a body, it might be predicted that BMR is predicted to be proportional to surface area, which is proportional to $M^{2/3}$, if all other variables (i.e. body temperature, thermal conductance) are equal. Empirical support for this theory was first provided by Rubner (1883). However, the now classic analyses of BMR by Kleiber (1932; 1961) reported an exponent significantly greater than 2/3, and an exponent of 3/4 was subsequently adopted. This exponent was later supported by Brody’s famous mouse-to-elephant curve (Brody 1945), as well as by both Benedict (1938) and Hemmingsen (1960), and remains in widespread use. However, Heusner’s (1991) analysis supported geometric scaling and Dodds *et al.* (2001) questioned the early empirical analyses. Additionally, phylogenetic (Hayssen and Lacy 1985; Elgar and Harvey 1987), ecological (McNab 1986; 1988a), and geographic (Lovegrove 2000) variation in the allometry of mammalian BMR has been reported.

Rather than attempting to argue the relative merits of one exponent over the other, this chapter approaches the problem from a different perspective. It asks how many species over what range of body mass would be required to obtain a scaling exponent of sufficient certainty to resolve the controversy. The 'true' allometric exponent could be determined if data were available for all ~4600 extant species of mammal (Nowak 1999), but this is virtually impossible, both because of the large number of species and because basal conditions may be unachievable in some species (Chapter 1). Therefore, 4600 artificial species were created, and sub-samples of selected size and body mass range were randomly taken for regression and analysis of the variability of the exponent. This is the first examination of the influences of sample size and body mass range on estimation of the allometric exponent.

Methods

Generation of BMR and body mass values for artificial species

The body masses of the 4600 artificial species were generated such that they matched the distribution of body masses of the 391 species compiled by Heusner (1991) (Figure 6.1), which was found to be significantly non-normal (Shapiro-Wilk test, $p < 0.05$). Transformation by $\log(\log(M))$ ($=M'$) resulted in the distribution satisfying the test for normality (Shapiro-Wilk test, $p = 0.13$), with a mean of 0.346 and a standard deviation of 0.198. 4600 values with a mean of 0.346 and standard deviation of 0.198 were then randomly generated. This was accomplished in the following manner: a relationship between z (the distance, measured in standard deviations, from the mean) and p (the proportion of the population with a mass more extreme than z) was constructed such that each value was generated by producing a random number between 0 and 0.5 (p), and converting this value to the number of standard deviations by which it differed from the mean using the relationship between z and p. For example, 5% of a normally distributed population lie greater than 1.96 standard deviations from the mean (Zar 1999) so a randomly generated p of 0.025 therefore corresponds with a z of 1.96. z was then randomly assigned a positive or negative sign, multiplied by 0.198 and added to 0.346 (the standard deviation and mean, respectively, of the distribution of M'). When these values were untransformed according to $10^\wedge(10^\wedge(M'))$, they

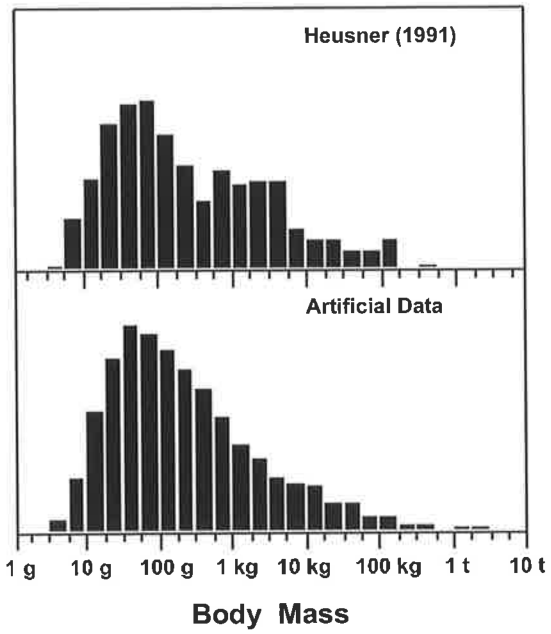

Figure 6.1. Body mass distribution of the 391 species compiled by Heusner (1991) and the 4600 artificial species (Artificial Data).

represented the body masses of the artificial species. In the example above, a p of 0.025 corresponds with mass of 10^(10^(0.346 ± 1.96 × 0.198)) g, which is equal to either 8.1 g or 25.8 kg, depending upon the sign assigned to z. A regression equation of the form log(BMR) = log(a) + b log(M) was used as a basis for determining BMR values of the artificial species. Residuals (BMR_{resid}) around the regression mean for the data from 391 species of real animals (Heusner 1991) were normally distributed with a mean of zero and a standard deviation of 0.177 (Figure 6.2). BMR_{resid} values for the artificial species were generated using the method described above for M, using a mean of zero and a standard deviation of 0.177. BMR values for artificial animals were then calculated by randomly assigning residuals according to $\log(BMR) = \log(a) + b \log(M) + BMR_{resid}$, where a was set to 1 and b was set to 2/3.

Analysis protocol

The philosophy behind the analysis was comparison of the allometric exponent calculated for a randomly selected subset of the data with the 'true' regression exponent for 4600 artificial species, which was 2/3. For a subset of the artificial species, log(BMR) was plotted against log(M), and the slope of the linear regression and the x-range of the data were recorded. A

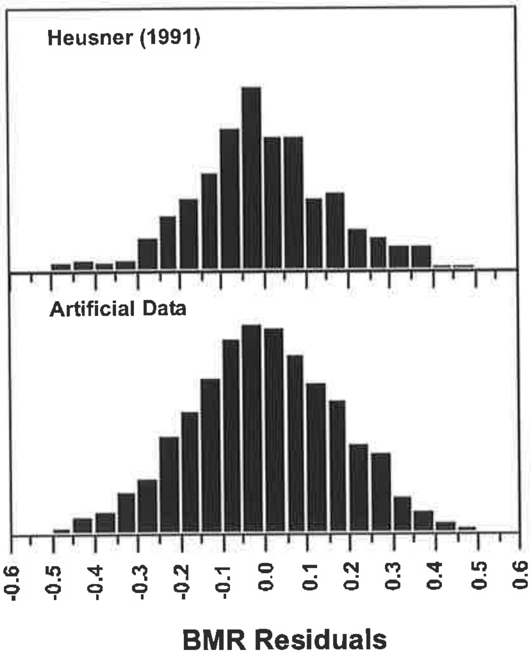

Figure 6.2. Frequency histogram of the BMR residuals of the 391 species compiled by (Heusner 1991) and the 4600 artificial species (Artificial Data).

PC program was written to accomplish these calculations (Appendix G). For each of six sample sizes (n = 5, 10, 20, 50, 100, and 250) the program worked by sequentially reading through the input file containing the 4600 data pairs and randomly excluding a proportion that was randomly set between 0 and 1. If the group that remained was of an appropriate size, regression statistics were calculated and stored in a separate file. This procedure was repeated approximately 50,000 times (range 41487 – 59440) for each of the six sample sizes. In practice, the procedure was undertaken with no restraint 25,000 times, after which the program was instructed to retain the exponent calculated for subsets that fell within specified criteria (e.g. x-range less than 3 orders of magnitude). This was necessary to ensure that the smallest and largest mass ranges were well represented relative to the middle mass ranges, because the middle mass ranges were massively over-represented following the initial 25,000 iterations.

Results

The mean slope of the regression of log(BMR) on log(M) for subsets of 5, 10, 20, 50, 100 and 250 species was similar to the slope on which the simulated data were based (0.67) in all cases (Figure 6.3). However, both the number of species included in the subset and the mass range of the subset had a marked influence on the spread of slopes around 0.67. In particular, increasing either sample size or the mass-range resulted in a reduction in the spread of the data set (manifested in minimum and maximum slopes that were more similar to 0.67) and a narrowing of the 2.5 to 97.5 percentile belt.

Discussion

The aim of this study was to determine the minimum sample size and body mass range necessary to distinguish between the exponents of 2/3 and 3/4, each of which is considered by various authors to be the appropriate exponent relating mammalian BMR and M. At sample sizes of five to 50, many of the subsample slopes were close to or greater than 3/4, particularly at smaller mass ranges (Figure 6.3). With a sample size of 100 and a mass range greater than three orders of magnitude, the subsample slopes clustered tightly around 2/3, and more than 95% of the subsamples had a slope lower than 3/4. Further increasing sample size to 250 resulted in further reduction in the variation in subsample slopes. With a sample size of 250 and a mass range greater than three orders of magnitude, none of the slopes were above 0.716. The relationship between sample size and x-range (Figure 6.4) shows that a sample size of around 50 spanning a mass range of three orders of magnitude is necessary for 95% of the slopes to be less than 0.75, and a sample size around 75 spanning a mass range around 5 orders of magnitude is necessary for 95% of the slopes to be less than 0.71 (the mid-point between 0.67 and 0.75). Given that recent compilations of mammalian BMR (Chapter 1; Heusner 1991; Lovegrove 2000) include approximately 600, 400, and 500 species, respectively, spanning more than five orders of magnitude variation in body mass, it is clear that they satisfy the criteria for producing a reliable estimate of the scaling exponent relating BMR and body mass for mammals. Knowledge of the 'true' allometric exponent is therefore within our grasp, and has been so for at least a decade. However, previous analyses (Kleiber 1932; Benedict 1938; Brody 1945; Hemmingsen 1960; Hayssen and Lacy 1985; McNab 1988a; Heusner 1991; Lovegrove 2000) have all been compromised by the inclusion of

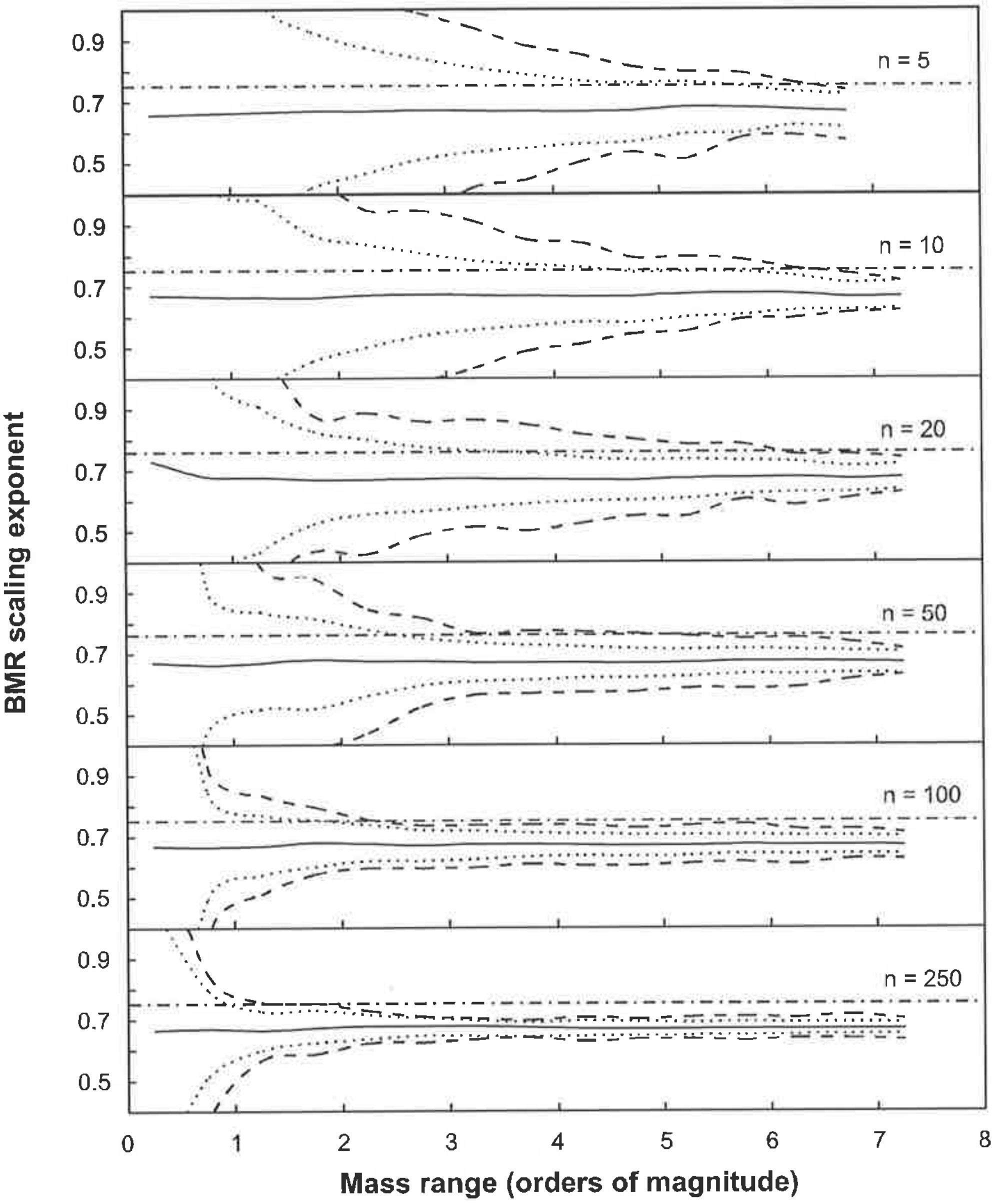

Figure 6.3. The effect of sample size and mass-range on the slope of a data subset drawn from an artificially constructed group of 4600 mammals. Each graph represents >25,000 subsets. The solid lines represent the mean slope, broken lines represent maximum and minimum slopes (— — —) or 2.5 and 97.5 percentiles (- - - - -). Horizontal lines (— - — - —) correspond with an exponent of 3/4.

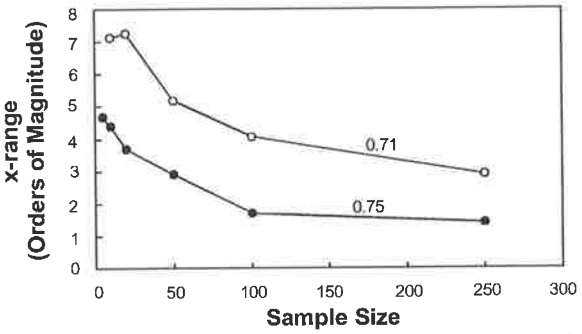

Figure 6.4. Relationship between sample size and the body mass range necessary for 95% of subsets randomly selected from 4600 'artificial species' to show a scaling exponent less than either 0.75 or 0.71 (which is intermediate between 0.75 and 0.67). The scaling exponent for the 4600 'artificial species' is 0.67.

non-basal measurements associated with microbial fermentation in the digestive systems of herbivores. The analysis presented in Chapter 1 is not similarly hindered, includes more species than any other, satisfies the requirements for estimation of the 'true' regression exponent as presented here, and concludes that the basal metabolic rate of mammals is proportional to $M^{2/3}$.

7. Phylogenetically informed regression methods do not systematically bias determination of the scaling exponent relating mammalian basal metabolic rate and body mass

Abstract

The relationship between the basal metabolic rate (BMR) and body mass (*M*) of mammals has been debated for almost seven decades, focusing on the value of the scaling exponent (b, where BMR $\propto M^{b}$) and the relative merits of b = 0.67 (geometric scaling) and b = 0.75 (quarter-power scaling). However, most analyses are not phylogenetically informed (PI). Recent evidence suggests that PI comparative analyses are unable to resolve the debate, because the value of the exponent is affected by phylogenetic history and phylogenies based on molecular data support geometric scaling, whilst phylogenies based on morphological data support quarter-power scaling. This paper approaches the problem from a different perspective using randomly generated evolutionary trees and a homogenous selection of randomly generated 'artificial species' together with a literature compilation of PI and conventional scaling exponent estimates for a variety of physiological and morphological data. It shows that PI regression methods do not systematically bias scaling exponent determination, suggesting that phylogenetically informed comparative analyses can help resolve the debate.

Introduction

A repeated occurrence in the comparative physiological literature is the dichotomy between geometric (b = 0.67, where $y = a M^{b}$ and M = body mass) and quarter-power (b = 0.75) scaling of basal metabolic rate (BMR: the rate at which an animal consumes energy when postabsorptive and at rest). Geometric scaling suggests that heat production is related through heat loss through the body surface, and was first empirically supported by Rubner (1883) and later by Heusner (1991). However, Max Kleiber's (1932; 1961) analyses of BMR reported an exponent significantly greater than 2/3, and a value of 3/4 was subsequently adopted. Brody's (1945) mouse-to-elephant curve further supported an exponent of 3/4, as did Benedict (1938) and Hemmingsen (1960). Quarter-power scaling has since become regarded as the physiological norm (e.g. Brown and West 2000; West *et al.* 2000), and a BMR scaling exponent of 3/4 remains in widespread use, despite lacking universal acceptance (Dodds *et al.* 2001).

Recently, conventional allometric analysis has been criticised because it assumes that each data point is independent of the rest and that correlations may be based on phylogenetic affinity rather than adaptation to the environment (Felsenstein 1985; Harvey and Pagel 1991; Garland *et al.* 1992). One approach to solve this problem is to carry out phylogenetically informed (PI) statistical procedures (e.g. Felsenstein 1985). However, regression using PI methods generally produce equations with larger standard errors (and confidence intervals) than conventional methods and they can produce significantly different equations (Garland *et al.* 1999; Garland and Ives 2000). For example, Symonds and Elgar (2002) calculated a PI regression exponent of BMR for 112 mammalian species using 33 different hypotheses of interordinal relationships constructed from molecular and morphological data. They found that recent molecular-based phylogenies tended to support a 0.67 exponent, whereas older phylogenies based on morphological data tended to suggest a 0.75 exponent. The phylogenetically informed results based on molecular phylogenies were more variable than those based on morphology and both were more variable than conventional methods. However, their specific conclusion relating to the debate surrounding the acceptance of 0.67 or 0.75 as the 'true' allometric exponent is confounded by the inclusion of a range of species for which a BMR may not be measurable (e.g. shrews that never rest and ruminants that are not post-absorptive: Chapter 1; McNab 1997). This problem limits the extent to which their analysis can be applied to the debate surrounding quarter-power and geometric scaling. Because many of the species with non-basal measurements are toward the upper extreme of the mass range (e.g. artiodactyls, *Elephas maximas*), an upward bias on the exponent is introduced and this can be expected to persist throughout the PI analyses. Furthermore, they fail to account for the positive correlation between body temperature and body mass (Chapter 1; Withers *et al.* 2000), which further increases the scaling exponent. Nevertheless, Symonds and Elgar (2002) do raise an important point concerning the impact that PI methods could potentially have on estimation of the 'true' BMR scaling exponent. One might argue, for example, that the use of PI methods might introduce a bias into estimation of the BMR scaling exponent and erroneously favour either geometric or quarter-power scaling. Such an argument might stem from the observations that (1) no single mammal lineage encompasses the full range of M observed within Mammalia and (2) BMR and M are highly correlated (M alone accounts for as much as 94 – 96% of the variation in BMR: Chapter 1). Hence, BMR and M are expected to be more similar within than between lineages. The scaling exponent relating BMR and M is therefore likely to contain a significant phylogenetic component.

Extension of this idea suggests that by removing the phylogenetic influence, PI methods may significantly alter the calculated exponent.

This study therefore aims to determine if PI methods bias estimation of the allometric scaling exponent relating mammalian M and BMR. This question is addressed by generating a series of 'artificial species' with similar variation in M and BMR as that observed for real mammals and placing these artificial species on a series of randomly generated phylogenies to investigate the role of phylogenetic arrangement on the allometric exponent. Furthermore, to determine if any bias inherent in the estimation of the BMR scaling exponent is a general observation and not limited to BMR, allometric exponents calculated by conventional and PI methods will be compared for a range of variables.

Methods

BMR and body mass generation for 'artificial species'

Body mass (M) and BMR values for 64 artificial species were generated such that they matched the distribution of M and BMR of the 391 species compiled by Heusner (1991). Briefly, Heusner's (1991) data were appropriately transformed so that the distributions of M and BMR residuals satisfied the test for normality. Data were then randomly generated to produce two data sets with the same mean and standard deviation as transformed BMR residuals and M and were then untransformed to produce BMR and M values for the artificial species. The relationship between BMR and M for the resulting 'artificial species' was based around a relationship of BMR = 1 $M^{0.67}$. Full details of data generation are provided in Chapter 6.

Comparison of conventional and PI regression: Artificial data

An arbitrary phylogeny, defined with a completely bifurcating branch structure culminating in 64 tips, was used for all phylogenetic analyses. Phylogenetically informed regression was undertaken using variations of three phylogenetic arrangements. In each case, internal and terminal branches were randomly varied in length between 0 and 1. (1) To examine if phylogenetic methods alter regression equations regardless of species arrangement, 100 phylogenetically informed regressions were conducted with individuals randomly assigned to branches. (2) Because mammal lineages include species within a discrete mass range rather than a range that encompasses the entire spectrum of mammalian body masses, 30 phylogenetically informed regressions were conducted with species divided into four clades according to mass, with individuals randomly assigned to tips within clades. (3) 30 phylogenetically informed regressions were conducted with individuals systematically assigned to tips according to body mass. Analysis (3) is a logical extension of analyses (1) and (2) and, although unlikely to represent any lineage of real mammals, allows examination of factors influencing phylogenetic regression results. Analyses (2) and (3) contain fewer regressions than analysis (1) because it was observed that the results changed little as sample size increased beyond 30. PI regressions were fitted according to Felsenstein's (1985) method of independent contrasts, implemented using the PDAP software suite distributed by T. Garland, Jr (Garland *et al.* 1993; 1999; Garland and Ives 2000). For PI regression, least-square regression slopes constrained to pass through the origin were calculated from scatter plots of the standardised contrasts for log(BMR) and log(M). A phylogenetically informed regression equation was then mapped back onto the original data by constraining a line with this slope to pass through the bivariate mean estimated by independent contrasts (e.g. Garland *et al.* 1993). For each regression a slope, standard error (SE) of the slope and upper and lower 95% confidence intervals (CI) were calculated.

Comparison of conventional and PI regression: Published data

A total of 95 conventional and PI regressions of physiological and ecological data were compiled from the literature (Chapter 4; Weathers and Siegel 1995; Christian and Garland 1996; Reynolds and Lee 1996; Autumn *et al.* 1997; Reynolds 1997; Degen *et al.* 1998; Bonine and Garland 1999; Blob 2000; Garland and Ives 2000; Nunn and Barton 2000; Tieleman and Williams 2000; Frappell *et al.* 2001). Variables considered include daily, resting and basal metabolic rate, respiratory variables (e.g. ventilation rate, tidal volume), cost of locomotion, sprint speed, and morphological variables (e.g. hindlimb proportions, body surface area). Values were only included if the results of conventional and PI regression were based on the same data and provided in a single paper. Conventional and PI regressions were then compared to determine if there are any systematic differences between scaling exponents estimated with the different methods.

Table 7.1. Comparison of regression (log(BMR) on log(body mass)) slope, slope standard error (SE) and upper and lower 95% confidence intervals (CI) calculated using conventional (Model 1) least-squares and phylogenetically informed (PI) methods for 64 simulated species (see text for details).

		Regression Method		
	Conventional	PI 1	PI 2	PI 3
Slope	0.662	0.662 ± 0.026	0.596 ± 0.069	0.642 ± 0.045
SE	0.024	0.025 ± 0.005	0.060 ± 0.012	0.088 ± 0.015
Lower 95% CI	0.613	0.613 ± 0.026	0.478 ± 0.079	0.465 ± 0.015
Upper 95% CI	0.710	0.710 ± 0.027	0.716 ± 0.065	0.819 ± 0.054
n		99	30	30

Note to Table 7.1. All PI methods use Felsenstein's (1985) independent contrasts. Measures obtained for PI regressions are presented as mean ± 1 standard deviation of results obtained for n phylogenies. PI 1 uses a tree with individuals randomly assigned to branches. PI 2 divides species into four clades according to mass, with individuals randomly assigned to tips within clades. PI 3 systematically assigned species to tips according to body mass.

Results and Discussion

Conventional least-squares regression of log(BMR) on log(M) for the 64 artificial species produced a relationship of BMR = 1.03 $M^{0.661}$. This relationship is, not surprisingly, very similar to the equation on which the artificial species are based (BMR = 1.0 $M^{0.67}$). Using PI methods with species randomly positioned on the phylogeny and branch lengths randomly varied between 0 and 1, regression slopes were normally distributed about a mean of 0.662 (Table 7.1, Figure 7.1). Compared using 95% confidence intervals for the slope, only 1 of 100 phylogenetically informed regressions differed significantly from the least-squares regression. This PI regression was unduly influenced by a single contrast, which included two of the larger simulated species (ranked 53 and 63 of 64 by M) and placed them each on very short branches. Diagnostic plots (see Garland *et al.* 1992) showed a correlation between the absolute value of contrasts and the standard deviation of contrasts for both log(BMR) and log(M), due primarily to the contrast discussed above, suggesting that branch lengths were not adequately standardising contrasts. Extension of this node's daughter branches to a length of 1 properly standardised the contrast, and recalculation of the PI regression yielded a slope of 0.669 with 95% confidence limits of 0.613-0.725. Somewhat surprisingly, PI methods did not

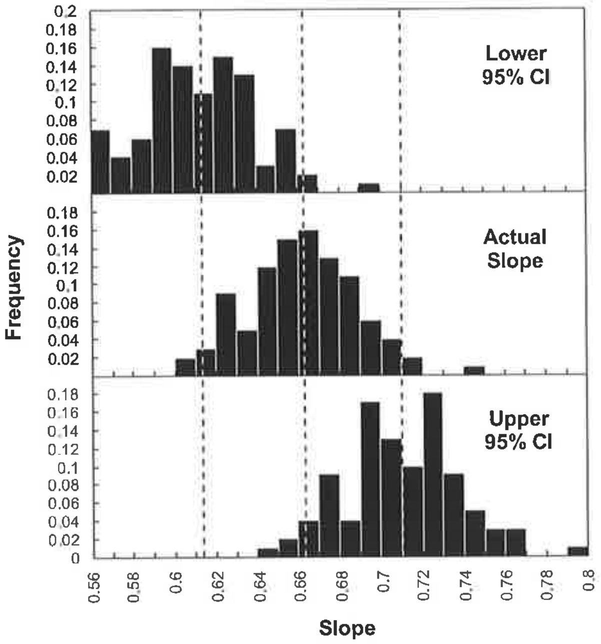

Figure 7.1. Frequency distributions of the log-log least squares regression slope and 95% confidence intervals of the slope for 99 rearrangements of 64 artificial species as determined using Felsenstein's (Felsenstein 1985) independent contrasts. The same 64 artificial species were used for all trials, however, for each trial the artificial species were randomly assigned to tree tips. Vertical broken lines represent (from left to right) the lower 95% CI, the mean and the upper 95% CI of the actual slope for the same 64 species, as calculated using conventional double-log least squares regression.

necessarily produce regressions with larger standard errors and wider confidence intervals than conventional least-squares regression (Table 7.1, Figure 7.1). However, this observation stems from the random assignment of species to the phylogeny. Species with similar traits were therefore no more likely to be related than species with less similar traits, approximating a situation where all species are equally related (star phylogeny). Deviation from a star phylogeny (firstly by grouping into four clades according to mass, and then by sorting according to mass) resulted in increased slope standard error estimates and widening of 95% CI's (Table 7.1). Put simply, the confidence intervals of PI regressions widen as species differences within a phylogenetic lineage decrease and differences between lineages increase.

Properly standardised PI regression using 160 rearrangements of three phylogenies did not produce any instances where the PI regression slope was significantly different from that obtained using conventional least-squares regression, although there was a non-significant tendency for PI regressions to have a shallower slope than conventional least-square regressions (Table 7.1). However, for the 95 regressions gathered from the literature

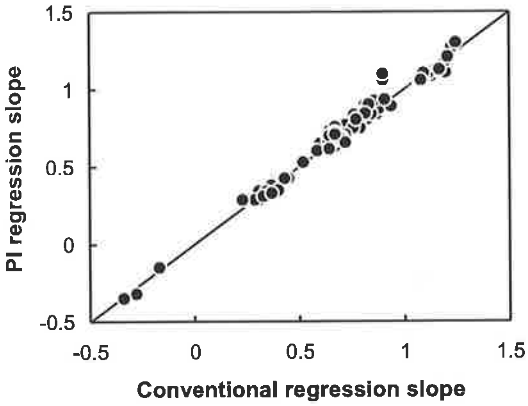

Figure 7.2. Relationship between allometric exponents determined using phylogenetically informed (PI) and conventional regressions. Data for the 95 regressions were taken from studies that provided both PI and conventional regression slopes. Solid line is a line of unity: conventional (b_c) and PI (b_{PI}) regression exponents are related according to the following equation: $b_{PI} = 1.01\ b_c + 0.01$, which is not significantly different from unity ($p > 0.05$).

(Figure 7.2), the slope of the line relating conventional and PI regression exponents is not significantly different from 1 (95% CI = 0.98 to 1.04), and the intercept is not significantly different from 0 (95% CI = -0.01 to 0.03). PI regression therefore does not introduce a systematic bias into allometric exponent calculation in either the artificial situations examined in this study, or in analysis of data obtained from real animals.

The present study aims to promote the case for the incorporation of phylogenetic information into allometric analyses by demonstrating that these methods neither systematically alter regression findings, nor necessarily widen confidence intervals compared to conventional methods. A finding, for example, that PI regression confidence intervals are considerably wider than the confidence intervals calculated using conventional methods is likely to be the result of overestimated degrees of freedom in the conventional model arising from the inclusion of many species representing few lineages. Similarly, a finding that conventional and PI exponents differ substantially is likely to be the result of the inclusion of several closely related species present toward the extremes of the mass range (e.g. artificially elevated or non-basal measurements of large animals such as artiodactyls). In a conventional model, these species would be weighted equally, but in a PI model, the shared ancestry of these influential data points reduces their weighting, and therefore also reduces their influence on the scaling exponent. These observations serve to emphasise the importance of ensuring

(1) that species are selected to maximize the variation present within lineages and (2) that non-independence problems are accounted for by completing subsequent analyses within a phylogenetic framework. With these considerations in mind, phylogenetically informed comparative analyses are likely to remain an indispensable tool for resolving the debate surrounding the value of the allometric scaling exponent relating mammalian body mass and basal metabolic rate. An interordinal analysis of the allometry of BMR, which used nested ANOVA (Harvey and Pagel 1991) to account for phylogenetic effects, for example, concluded that M accounted for 99% of the variation in body temperature normalised BMR and strongly supported a scaling exponent of 2/3 (Chapter 1).

8. Allometric analysis beyond heterogeneous regression slopes: Use of the Johnson-Neyman technique in comparative biology

Abstract

Allometric data for different groups are most often compared using analysis of covariance (ANCOVA), a statistical procedure that compares treatment means (groups) after accounting for and removing their relationship with a covariate (often body mass). A requirement of ANCOVA is that the relationship with the covariate is uniform across groups, i.e. the regression slopes must be identical. This chapter describes a procedure (The Johnson-Neyman technique) that is applied following a finding of significantly heterogeneous regression slopes and allows for identification of the range of x-values at which there is a significant difference between groups. This allows potentially valuable information to be gleaned from data that might otherwise have been overlooked because of statistical limitations.

Introduction

Allometry (or scaling) is a common technique used to evaluate and compare physiological, morphological and other variables in organisms of different size. The relationship between many variables (y) and body mass (x) is well described by a power function of the form $y = a\,x^{b}$. Typically, the procedure involves log-transforming both the variable and body mass and calculating a linear regression of the form $\log(y) = \log(a) + b \log(x)$. An advantage of log-linear analysis is that it allows calculation of associated 95% confidence intervals for the regression mean and 95% prediction intervals. Furthermore, allometric regressions for two or more groups can be compared. This is often accomplished by analysis of covariance (ANCOVA: Fisher 1932), a statistical procedure that combines analysis of variance (ANOVA) and analysis of variance of regressions (ANOVAR) to compare treatment means (groups) after accounting for and removing their relationship with the covariate (often body mass). Generally, ANCOVA is more appropriate for most data than is ANOVA carried out on ratios of the variable and covariate, because many variables do not have an isometric relationship with body mass (Packard and Boardman 1987; 1988; 1999).

A requirement of ANCOVA is that the relationship with the covariate is uniform across groups, i.e. the regression slopes (b) must be identical. In practice, prior to commencing ANCOVA it must therefore be demonstrated that the slopes are not significantly different between groups. When the slopes differ, regression elevations (a) cannot be statistically compared using ANCOVA (Zar 1999). The standard texts on allometry (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Brown and West 2000) provide little advice on how to continue analysis following a finding of heterogeneous regression slopes, yet it appears repeatedly in the literature. Of the 88 papers published in *Physiological and Biochemical Zoology* in 2000, for example, 25 made use of ANCOVA in various forms. Of these 25 papers, six either reported, made mention of, or appeared to show heterogeneous regression slopes. These findings were dealt with in many ways: some authors appear to have ignored the result and continued statistical analysis of regression elevations, some continued analysis without reporting significance and some did not continue analysis beyond this point.

Several analyses are available for data demonstrating heterogeneous regression slopes. Firstly, and most simply, such a finding can be regarded as evidence of a significant treatment effect (Cochran 1957; Packard and Boardman 1987). An experimenter is therefore able to conclude that the groups are significantly different. Zar (1999) details a procedure where points on regression lines with heterogeneous slopes are compared if they have identical x-values. This allows systematic, though time consuming, examination of the nature of inter-group differences. Hendrix *et al.* (1982) describe a similar procedure for multiple comparisons. Groups are first compared pair-wise and those that are found not to have significantly different slopes are compared using ANCOVA. Next, slopes are compared in groups of three, followed by ANCOVA comparison where appropriate. The procedure continues in this manner until the slopes of all groups are compared simultaneously. Where groups are found to have significantly different slopes, group elevations are compared at multiple values of the covariate. Other procedures allow examination of the nature of the differences between regression slopes for multiple comparisons (Robson and Atkinson 1960). Although other methods are available (e.g. Abelson 1953; Potthoff 1964; Rogosa 1980), they are extensions of the procedure that is the subject of this comment, namely the Johnson-Neyman technique (Johnson and Neyman 1936). This technique has previously been applied in the fields of medical and behavioural science, sociology and ecology (e.g. Huitema 1980; Dorsey and Soeken 1996; Gillanders 1997; Leon *et al.* 1998) and allows identification of the range of x-values for which there is no significant difference between groups (henceforth referred to as 'the region of non-significance'). The applicability of this technique is demonstrated here using three sets of simulated data, one set of real data gathered from the

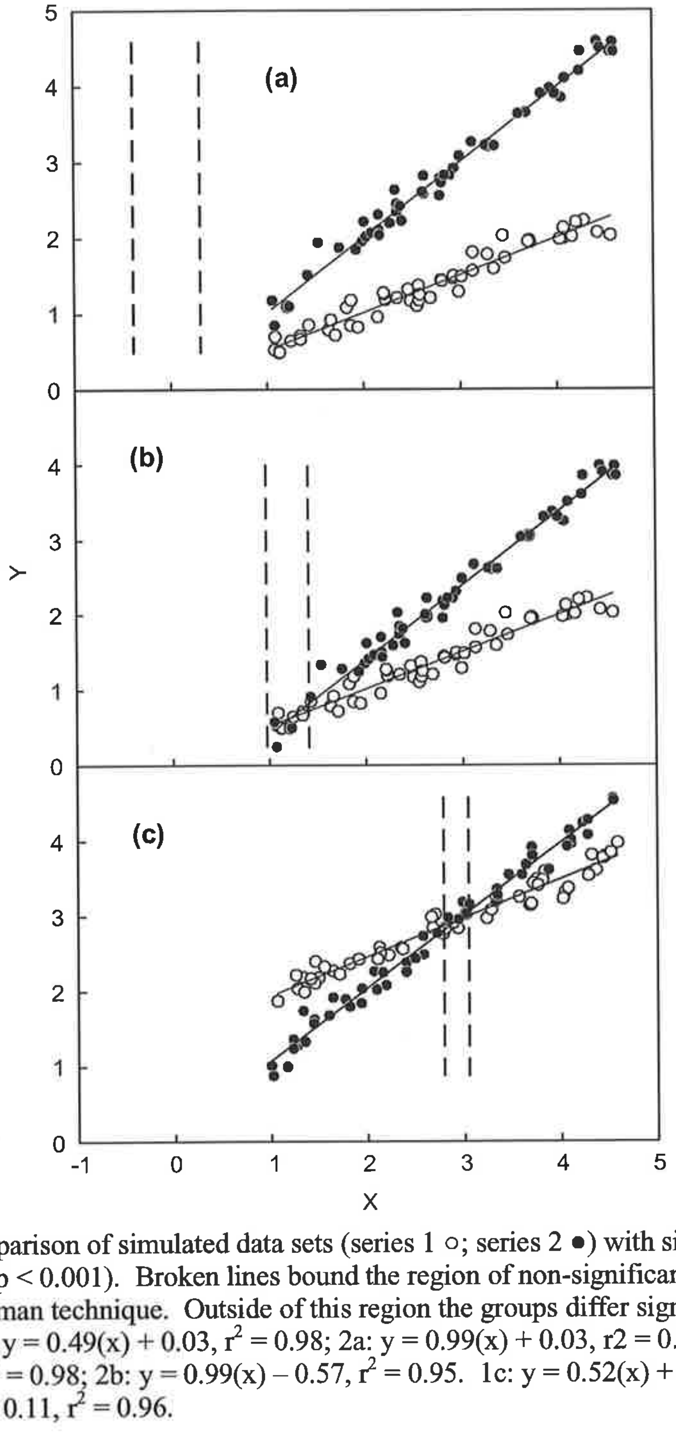

Figure 8.1. Comparison of simulated data sets (series 1 ○; series 2 ●) with significantly different slopes ($p < 0.001$). Broken lines bound the region of non-significance determined by the Johnson-Neyman technique. Outside of this region the groups differ significantly ($p = 0.05$). Series 1a: $y = 0.49(x) + 0.03$, $r^2 = 0.98$; 2a: $y = 0.99(x) + 0.03$, r2 = 0.95. 1b: $y = 0.49(x) + 0.03$, $r^2 = 0.98$; 2b: $y = 0.99(x) - 0.57$, $r^2 = 0.95$. 1c: $y = 0.52(x) + 1.42$, $r^2 = 0.99$; 2c: $y = 0.97(x) + 0.11$, $r^2 = 0.96$.

literature, and reanalysis of a recent publication that reported heterogeneous regression slopes (Seymour and Blaylock 2000). This publication was chosen because it features compilation and analysis of data from multiple published sources and because the authors provide the raw data on which it is based.

Data Simulation

A regression equation of the form y = a + b(x) was used as a basis for all simulated data sets. Two groups (series 1 and 2) were constructed for each comparison. Residuals (y_{resid}) around the regression mean were normally distributed with a standard deviation of 0.13. This is the standard deviation of residuals around a regression of log(BMR) on log(body mass) for 54 mesic-adapted burrowing mammals, where BMR is basal metabolic rate (mL O_2 min^{-1}) and body mass is in g (Chapter 4). For each data set, 50 x-values within a specified range (representing body masses of 10 g to 40 kg) were randomly generated. y values were then calculated using randomly assigned residuals as: $y = a + b(x) + y_{resid}$

Simulated data set 1: different slopes, same intercept

The least-squares regressions for the data series in this comparison have significantly different slopes ($F_{1,96} = 380$, $p < 0.001$) (Figure 8.1a). If we were to ignore this violation of the assumptions of ANCOVA and compare elevations we would conclude that the regressions differ in elevation also (ANCOVA $F_{1,97} = 589$, $p < 0.001$). As the slopes of the two data series compared in this example are not the same, it follows that for a single value of x (in this case, x = 0), the regression lines will cross and both regressions will predict an identical value of y. The magnitude of the difference in elevation found by ANCOVA therefore varies with x. For x = 0 the regressions have an identical elevation; for x > 0, series 2 has a greater elevation than series 1; and for x < 0 series 1 has a greater elevation than series 2. In many cases it may be of interest to know for which values of x the elevations of the regressions of series 1 and 2 are significantly different. The potential use of this knowledge is obvious in the present example where the series have what appear to be quite different elevations (Figure 8.1a) but violation of ANCOVA assumptions prevents us from making statements about the significance of this observation. Calculation of the region of non-significance using the Johnson-Neyman technique shows that for ($-0.387 \leq x \leq 0.310$) the elevations of the regression equations are not significantly different ($p = 0.05$). Therefore, over the range of

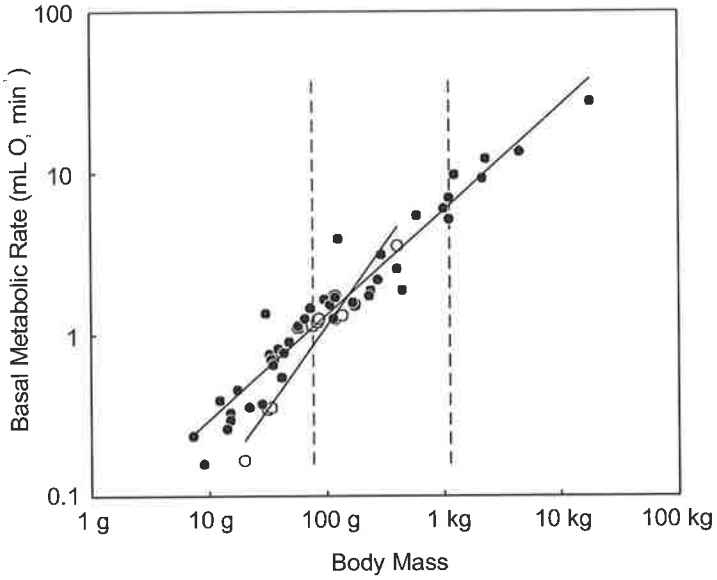

Figure 8.2. Real data relating body mass (x) and basal metabolic rate mL O_2 min^{-1} (y) for fossorial (○) and semi-fossorial (●) arid-adapted mammals. Broken lines bound the region of non-significance as determined using the Johnson-Neyman technique. Outside of this region the groups differ significantly in elevation. Equations of the linear least-squares regression lines: Fossorial: $\log(y) = 1.02 \log(x) - 1.98$, $r^2 = 0.94$. Semi-fossorial: $\log(y) = 0.65 \log(x) - 1.17$, $r^2 = 0.94$.

data in this comparison, series 2 is shown to have a significantly greater elevation than series 1 ($p = 0.05$).

Simulated data set 2: different slopes, overlap at edge of x-range

Figure 8.1b shows a situation similar to Figure 8.1a in that the majority of series 2 shows a greater elevation than the majority of series 1. An important difference, however, is that the smallest x-values of series 1 and 2 overlap. If we were to compare linear least-squares regressions of these series we would find that they differ significantly in slope ($F_{1,96} = 380$, $p < 0.001$) and elevation (ANCOVA $F_{1,97} = 186$, $p < 0.001$). Ignoring the violation of the homogeneity of regression slopes assumption of ANCOVA would therefore lead us to conclude that series 2 has a significantly greater elevation than series 1. This is not surprising because most of the values for series 2 are above those of series 1. However, at the smallest x-values the series appear to show sufficient overlap to suggest that this conclusion may be misleading, at least for some x-values. Calculation of the region of non-significance using the Johnson-Neyman technique shows that for ($0.972 \leq x \leq 1.410$) the elevations of the regression equations are not significantly different ($p = 0.05$). Therefore we can conclude that for x-values greater than 1.410, series 2 has a greater elevation that series 1.

Simulated data set 3: different slopes, overlap in middle of x-range

Figure 8.1c shows data that have an overlap similar to the series from Figure 8.1b, but in this case the x-value at which y predicted by the two regression equations is the same ($x = 2.919$) is close to the middle of the x-ranges of the data series. When compared, we find that series 1 and 2 differ in slope ($F_{1,96} = 410$, $p < 0.001$) but not in elevation (ANCOVA $F_{1,97} = 1.75$, $p = 0.19$). Again, this result appears to be misleading. At both low and high x-values the series appear to be clearly separated. The Johnson-Neyman technique supports this intuitive conclusion by finding that for ($2.797 \leq x \leq 3.045$) the elevations of the regression equations are not significantly different ($p = 0.05$). Therefore, for $x < 2.797$ series 1 has a greater elevation than series 2 and for $x > 3.045$ series 2 has a greater elevation than series 1.

Real data: BMR of arid-adapted, burrowing mammals

I compared the basal metabolic rates (BMR) of two groups of arid-adapted burrowing mammals using data sourced from the peer-reviewed literature (Chapter 4). The groups compared were fossorial mammals, which forage beneath the surface and spend almost all of their lives within burrow systems, and semi-fossorial mammals, which forage on the surface and construct burrow refuges that are inhabited periodically. To enable calculation of linear regression equations, both BMR (mL O_2 min^{-1}) and body mass (g) were log-transformed. The resultant regressions were compared using ANCOVA with log(body mass) as the covariate (Figure 8.2). The regressions of log(BMR) on log(body mass) for fossorial and semi-fossorial mammals differ in slope ($F_{1,50} = 10.1$, $p = 0.003$). The Johnson-Neyman technique showed that for ($1.885 \leq x \leq 3.041$) the elevations of the regression equations are not significantly different ($p = 0.05$). Outside of this region the elevations of the group regression means are significantly different. This result was particularly interesting because the limits of the region of non-significance separated only four species from the remaining 50. However, low and labile body temperatures characterise these four fossorial animals, whilst the remaining fossorial and semi-fossorial species maintain higher, more stabile body temperatures. The high slope of the log-linear regression describing the relationship between body mass and BMR for fossorial mammals (1.02) is therefore the result of a grouping that is both

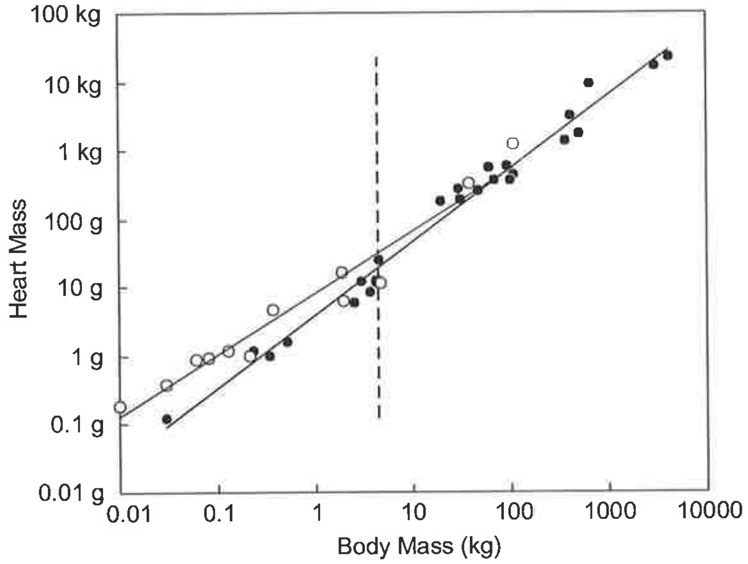

Figure 8.3. Real data relating body mass (x) and heart mass (y) for birds (○) and mammals (●) (Seymour and Blaylock 2000). Vertical dashed line represents the lower limit of the region of non-significance as determined using the Johnson-Neyman technique. To the left of this line the groups differ significantly in elevation. Equations of the linear least-squares regression lines: Birds: $\log(y) = 0.90 \log(x) + 0.91$, $r^2 = 0.95$; Mammals: $\log(y) = 1.07 \log(x) + 0.59$, $r^2 = 0.98$.

statistically and biologically inappropriate. Exclusion of the four smallest species from regression calculation for the remaining 50 species results in a regression slope consistent with the widely accepted observation that mass-specific BMR decreases with increasing body mass.

Real Data: Heart masses of mammals and birds

In their study of the principle of Laplace and scaling of ventricular wall stress and blood pressure, Seymour and Blaylock (2000) found that the linear regressions relating log-transformed heart mass to log-transformed body mass (as the covariate) for mammals and birds had significantly different slopes. They noted that this prevented testing for significant differences in elevation but stated that "the bird hearts were obviously heavier within the range of similar body mass" and "the scaling factor was twice as high at a body mass of 1 kg, but the data converge in larger species". The Johnson-Neyman technique showed that, at $p = 0.05$, regression elevations are not significantly different at masses above 4.26 kg (Figure

8.3), thus confirming the conclusion that the hearts of flightless birds are not significantly larger than similarly sized mammals. Given that the hearts of small (< 4.26 kg) birds, the majority of which are capable of flight, are significantly larger than those of similarly sized mammals, it therefore seems appropriate to regress fliers (small birds) and non-fliers (small birds and large mammals) separately. Similarly, the blood pressures of mammals and birds are similar at large masses and diverge at small masses (Seymour and Blaylock 2000). The large hearts and high blood pressures of small birds therefore appear to be associated with the increased metabolic demands of flight.

Discussion

The Johnson-Neyman technique provides a useful extension of a more widely used technique (ANCOVA). Where appropriate, it allows analysis to continue following violation of the assumption of homogeneity of regression slopes. Potentially valuable information may thereby be gleaned from data that might otherwise have been of little interest or conceptual value. It must be remembered, however, that aside from the assumption of homogenous regression slopes, the Johnson-Neyman technique requires satisfaction of similar assumptions to ANCOVA. The major assumptions are summarised by Huitema (1980):

1. The residuals of the within-group regressions of y on x are independent, and individuals have been randomly selected from a specified population and randomly assigned to groups.
2. The residuals are normally distributed.
3. The residuals have homogeneous variance for each value of x.
4. The residuals have homogeneous variance across treatment groups.
5. The regression of y on x is linear
6. The levels of the covariate are fixed.
7. The covariate is measured without error.

At this point it is important to note that because the Johnson-Neyman technique must satisfy similar assumptions as ANCOVA, comparison without the use of phylogenetically informed statistical methods is likely to be open to the same criticisms currently levelled at conventional ANOVA and ANCOVA (Garland *et al.* 1993). Assumption 1 in particular is likely to be violated when analysing data gathered from different species. This is because closely related species are likely to be more similar than distantly related species, and may therefore be expected to have more similar y-values (and hence, y-residuals). Furthermore, species cannot be considered as having been randomly assigned to groups when the grouping is a consequence of their phylogenetic heritage.

When applying the Johnson-Neyman technique to a comparison, one must also bear in mind that this test is somewhat more conservative than the heterogeneity of regression slope test. Therefore, when regression slopes are found to be significantly different, it may not always be possible to calculate a region of non-significance within the range of available data. Such an occurrence is most common when the calculated p-value for the homogeneity of regression test is close to α. However, this potential shortcoming does not detract from the usefulness of the Johnson-Neyman technique. For example, such a situation may arise because the analysis has insufficient statistical power to resolve an elevational difference between the groups. If this is the case, this shortcoming can be addressed. Although reanalysis is not always practical or possible, statistical power can be increased in either of two non-exclusive ways: (1) by increasing sample size and/or x-range; (2) by ensuring that sample sizes of the groups are equivalent.

Given that the situations in which the Johnson-Neyman technique is useful are readily identified (if the regression slopes differ, then go ahead) and it produces results that are easy to visualise and interpret, a single hurdle remains before it can be widely accepted. To my knowledge, no commercially available statistical packages can be used to perform this test. Huitema (1980) presents an excellent explanation of the procedures required for both ANCOVA and the Johnson-Neyman technique, but this book is no longer in print. The equations necessary to calculate the region of non-significance are therefore included below and a Microsoft Excel 2000 spreadsheet that performs both ANCOVA and the Johnson-Neyman technique has been made available for distribution via email.

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Calculation of the region of non-significance

The limits of the region of non-significance are calculated according to

$$X_{lower} = \frac{-B-\sqrt{B^2-AC}}{A}$$

$$X_{upper} = \frac{-B+\sqrt{B^2-AC}}{A}$$

where

$$A = \frac{-F_{(\alpha,1,N-4)}}{N-4}(SSres_i)\left(\frac{1}{\sum x_1^2}+\frac{1}{\sum x_2^2}\right)+(b_1-b_2)^2$$

$$B = \frac{F_{(\alpha,1,N-4)}}{N-4}(SSres_i)\left(\frac{\overline{X}_1}{\sum x_1^2}+\frac{\overline{X}_2}{\sum x_2^2}\right)+(a_1-a_2)(b_1-b_2)$$

$$C = \frac{-F_{(\alpha,1,N-4)}}{N-4}(SSres_i)\left(\frac{N}{n_1 n_2}+\frac{\overline{X}_1^2}{\sum x_1^2}+\frac{\overline{X}_2^2}{\sum x_2^2}\right)+(a_1-a_2)^2$$

$$SSres_i = \left(\sum y_1^2-\frac{\left(\sum xy_1\right)^2}{\sum x_1^2}\right)+\left(\sum y_2^2-\frac{\left(\sum xy_2\right)^2}{\sum x_2^2}\right)$$

$F_{(\alpha,1,N-4)}$ = critical value of F statistic at α for 1 and $N-4$ degrees of freedom

N = total number of observations = $n_1 + n_2$

n_1, n_2 = number of observations in groups 1 and 2, respectively

$\overline{X}_1$, $\overline{X}_2$ = covariate means for groups 1 and 2, respectively

a_1, a_2 = regression intercepts for groups 1 and 2, respectively

b_1, b_2 = regression slopes for groups 1 and 2, respectively

The quantities $\sum x_1^2$, $\sum x_2^2$, $\sum y_1^2$, $\sum y_2^2$, $\sum xy_1$, and $\sum xy_2$ are calculated according to the following equations:

$$\sum x_1^2 = \sum X_1^2 - \frac{\left(\sum X_1\right)^2}{n_1}$$

$$\sum y_1^2 = \sum Y_1^2 - \frac{\left(\sum Y_1\right)^2}{n_1}$$

$$\sum xy_1 = \sum XY_1 - \frac{\left(\sum X_1\right)\left(\sum Y_1\right)}{n_1}$$

$$\sum x_2^2 = \sum X_2^2 - \frac{\left(\sum X_2\right)^2}{n_2}$$

$$\sum y_2^2 = \sum Y_2^2 - \frac{\left(\sum Y_2\right)^2}{n_2}$$

$$\sum xy_2 = \sum XY_2 - \frac{\left(\sum X_2\right)\left(\sum Y_2\right)}{n_2}$$

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Appendix A. Body mass (*M*), body temperature (T_b) and basal metabolic rate (BMR) of mammals

		M (g)	T_b (°C)	BMR (mL O_2 h^{-1})	Reference
Artiodactyla (7)		**5088**	**38.1**	**13632**	
Antilocapridae	*Antilocapra americana*	37800		9318	Wesley *et al.* (1973)
Bovidae	*Connochaetes taurinus*	196500		41242	Rogerson (1968)
Bovidae	*Ovis canadensis*	69125		19120	Chappel and Hudson (1978)
Cervidae	*Alces alces*	325000	38.6	51419	Renecker and Hudson (1986)
Cervidae	*Capreolus capreolus*	21500		8308	Weiner (1977)
Cervidae	*Odocoileus virginianus*	58588	39	25609	Silver *et al.* (1969); Demarais *et al.* (1986)
Tayassuidae	*Pecari tajacu*	20500	37.5	5945	Zervanos (1975)
Carnivora (48)		**4452**	**37.5**	**1244**	
Canidae	*Alopex lagopus*	3600	38.6	1374	Casey *et al.* (1979)
Canidae	*Canis latrans*	10000	37	2687	Golightly and Ohmart (1983)
Canidae	*Canis mesomelas*	7720	38	3860	Downs *et al.* (1991)
Canidae	*Cerdocyon thous*	5444	38.2	1524	Hennemann *et al.* (1983)
Canidae	*Fennecus zerda*	1215	38.8	583	Maloiy *et al.* (1982)
Canidae	*Vulpes macrotis*	1769	38	887	Golightly and Ohmart (1983)
Canidae	*Vulpes vulpes*	4440	38.7	2442	McNab (1970)
Canidae	*Vulpes vulpes alascensis*	4725		2481	Irving *et al.* (1955)
Felidae	*Acinonyx jubatus*	37900	39	8982	Taylor and Rowntree (1973)
Felidae	*Felis concolor*	37200	37.6	8842	McNab (2000b)
Felidae	*Felis pardalis*	10500	38.0	3126	McNab (2000b)
Felidae	*Felis rufus*	9400		4220	McNab (2000b)
Felidae	*Felis serval*	10100	36.5	3137	McNab (2000b)
Felidae	*Felis wiedii*	3600	38.0	937	McNab (2000b)
Felidae	*Felis yagouaroundi*	8400	38.4	1737	McNab (2000b)
Felidae	*Panthera leo*	98000	37.9	16954	McNab (2000b)
Felidae	*Panthera onca*	50400		11189	McNab (2000b)
Felidae	*Panthera tigris*	137900	37.5	23995	McNab (2000b)
Herpestidae	*Galerella sanguinea*	540	38.7	410	Kamau *et al.* (1979)
Herpestidae	*Herpestes javanicus*	611	39.8	403	Ebisu and Whittow (1976)
Herpestidae	*Suricata suricatta*	850	36.3	310	Lovegrove (2000)
Hyaenidae	*Hyaena hyaena*	34300		5728	McNab (2000b)
Hyaenidae	*Proteles cristatus*	8100	36.4	2194	McNab (2000b)
Mustelidae	*Eira barbara*	2950	38.4	1221	McNab (1995)
Mustelidae	*Gulo gulo*	12700		5694	Heusner (1991)
Mustelidae	*Lutra lutra*	10000	38.1	4500	Iversen (1972); Kruuk *et al.* (1997)
Mustelidae	*Martes americana*	900	38	595	Worthen and Kilgore (1981)
Mustelidae	*Martes martes*	920		717	Heusner (1991)
Mustelidae	*Meles meles*	11050		2984	Iversen (1972)
Mustelidae	*Mustela erminea*	75	39.6	165	Casey *et al.* (1979)
Mustelidae	*Mustela frenata*	225	39	241	Heusner (1991)
Mustelidae	*Mustela vison*	660	39	488	Farrell and Wood (1968); Wamberg *et al.* (1996)
Mustelidae	*Spilogale putorius*	624	36.4	300	Knudsen and Kilgore (1990)

		M (g)	T_b (°C)	BMR (mL O_2 h^{-1})	Reference
Mustelidae	*Taxidea taxus*	9000	38.0	2700	Harlow (1981)
Procyonidae	*Ailurus fulgens*	5740	37.6	878	McNab (1995)
Procyonidae	*Bassariscus sumichrasti*	1280	38.8	634	McNab (1995)
Procyonidae	*Nasua narica*	3670	38.6	1207	McNab (1995)
Procyonidae	*Nasua nasua*	4000	36.4	992	McNab (1995)
Procyonidae	*Potos flavus*	2343	36.1	796	McNab (1995)
Procyonidae	*Procyon cancrivorus*	1160		464	Scholander *et al.* (1950)
Procyonidae	*Procyon lotor*	5075	38.0	1599	McNab (1995)
Ursidae	*Ursus ursinus*	6696		844	McNab (1992b)
Viverridae	*Arctictis binturong*	14280	36.7	2285	McNab (1995)
Viverridae	*Arctogalidia trivirgata*	2010	36.2	553	McNab (1995)
Viverridae	*Fossa fossana*	2260	37.9	906	McNab (1995)
Viverridae	*Genetta tigrina*	1698		747	Henneman and Konecny (1980)
Viverridae	*Nandinia binotata*	4270	37.4	863	McNab (1995)
Viverridae	*Paradoxurus hermaphroditus*	3160	36.5	760.0	McNab (1995)
Chiroptera (77)		**18.8**	**34.4**	**25.11**	
Emballonuridae	*Peropteryx macrotis*	5	34.4	11.6	Genoud *et al.* (1990)
Emballonuridae	*Saccopteryx bilineata*	7.8	35.5	14.5	Genoud and Bonaccorso (1986)
Hipposideridae	*Hipposideros galeritus*	8.5	31.9	9.4	McNab (1989)
Hipposideridae	*Rhinonycteris aurantius*	8.27	36.1	16.2	Baudinette *et al.* (2000)
Megadermatidae	*Macroderma gigas*	148	37	139.1	McNab (1969)
Molossidae	*Eumops perotis*	56	32.6	39.8	McNab (1969)
Molossidae	*Molossus molossus*	15.6	31.4	22.5	McNab (1969)
Molossidae	*Tadarida brasiliensis*	16.9	36	20.3	Geiser (1988b)
Mormoopidae	*Mormoops blainvilli*	8.6	32	8.0	Rodriguez-Duran (1995)
Mormoopidae	*Mormoops megalophylla*	16.5	36.9	24.4	Bonaccorso *et al.* (1992)
Mormoopidae	*Pteronotus davyi*	9.4	38.8	15.3	Bonaccorso *et al.* (1992)
Mormoopidae	*Pteronotus parnellii*	19.2	36.4	30.7	Bonaccorso *et al.* (1992)
Mormoopidae	*Pteronotus personatus*	14	37.5	23.0	Bonaccorso *et al.* (1992)
Mormoopidae	*Pteronotus quadridens*	4.9	31	6.1	Rodriguez-Duran (1995)
Natalidae	*Natalus tumidirostris*	5.4	32.2	8.3	Genoud *et al.* (1990)
Noctilionidae	*Noctilio albiventris*	27	32	31.6	McNab (1969)
Noctilionidae	*Noctilio leporinus*	61	33.8	70.8	McNab (1969)
Phyllostomidae	*Anoura caudifera*	11.5	36.5	42.7	McNab (1969)
Phyllostomidae	*Artibeus fimbriatus*	63.9		78.0	Cruz-Neto *et al.* (2001)
Phyllostomidae	*Artibeus jamaicensis*	45.2	36.4	76.8	McNab (1969)
Phyllostomidae	*Artibeus lituratus*	70.1	37.3	108.0	McNab (1969)
Phyllostomidae	*Carollia perspicillata*	14.9	36.4	43.1	McNab (1969)
Phyllostomidae	*Chiroderma doriae*	19.9		31.1	Cruz-Neto *et al.* (2001)
Phyllostomidae	*Chrotopterus auritus*	96.1	37.2	141.3	McNab (1969)
Phyllostomidae	*Desmodus rotundus*	29.4	35	34.7	McNab (1969)
Phyllostomidae	*Diaemus youngi*	36.6	31.1	37.3	McNab (1969)
Phyllostomidae	*Diphylla ecaudata*	27.8	32.4	38.6	McNab (1969)
Phyllostomidae	*Erophylla bombifrons*	16.1	32	17.7	Rodriguez-Duran (1995)
Phyllostomidae	*Glossophaga soricina*	9.6	35.5	29.4	McNab (1969)
Phyllostomidae	*Koopmania concolor*	19.7	35.3	39.8	McNab (1969)
Phyllostomidae	*Leptonycteris curasoae*	22	35.7	44.0	McNab (1969)
Phyllostomidae	*Macrotus californicus*	11.7	35	14.6	Bell *et al.* (1986)
Phyllostomidae	*Monophyllus redmani*	8.7	34	11.1	Rodriguez-Duran (1995)

		M (g)	**T_b** (°C)	**BMR** (mL O_2 h^{-1})	**Reference**
Phyllostomidae	*Phyllostomus discolor*	33.5	34.6	47.9	McNab (1969)
Phyllostomidae	*Phyllostomus elongatus*	35.6		38.8	McNab (1969)
Phyllostomidae	*Phyllostomus hastatus*	84.2	34.7	100.2	McNab (1969)
Phyllostomidae	*Platyrrhinus lineatus*	21.9	36.4	44.9	McNab (1969)
Phyllostomidae	*Rhinophylla fischerae*	9.5		16.2	McNab (1969)
Phyllostomidae	*Rhinophylla pumilio*	9.5	34.7	18.6	McNab (1969)
Phyllostomidae	*Sturnia tildae*	20.5		39.9	Cruz-Neto *et al.* (2001)
Phyllostomidae	*Sturnira lilium*	21.9	36.4	53.2	McNab (1969)
Phyllostomidae	*Tonatia bidens*	27.4	37	55.1	McNab (1969)
Phyllostomidae	*Uroderma bilobatum*	16.2	35.1	31.6	McNab (1969)
Phyllostomidae	*Vampyressa pusilla*	8.8		18.6	Cruz-Neto *et al.* (2001)
Pteropodidae	*Cynopterus brachyotis*	37.4	36.5	47.5	McNab and Bonaccorso (2001)
Pteropodidae	*Dobsonia anderseni*	241.4	36.4	174.0	McNab and Bonaccorso (2001)
Pteropodidae	*Dobsonia minor*	73.7	36.5	74.4	McNab and Bonaccorso (2001)
Pteropodidae	*Dobsonia moluccensis*	404.3	36.8	367.9	McNab and Bonaccorso (2001)
Pteropodidae	*Dobsonia praedatrix*	179.5	37.1	142.5	McNab and Bonaccorso (2001)
Pteropodidae	*Eonycteris spelaea*	51.6	34	48.0	McNab and Bonaccorso (2001)
Pteropodidae	*Macroglossus minimus*	15.9	36.2	18.5	McNab and Bonaccorso (2001)
Pteropodidae	*Megaloglossus woermanni*	12.4		21.7	Lovegrove (2000)
Pteropodidae	*Melonycteris melanops*	53.3	34.9	43.3	McNab and Bonaccorso (2001)
Pteropodidae	*Nyctimene albiventer*	30.9	35.9	27.3	McNab and Bonaccorso (2001)
Pteropodidae	*Nyctimene cyclotis*	40.4	36	64.6	McNab and Bonaccorso (2001)
Pteropodidae	*Nyctimene major*	13.6	33	20.4	Hosken (1997)
Pteropodidae	*Paranyctimene raptor*	23.6	33.8	24.5	McNab and Bonaccorso (2001)
Pteropodidae	*Pteropus giganteus*	562.2	36.7	290.7	McNab and Bonaccorso (2001)
Pteropodidae	*Pteropus hypomelanus*	520.8	35.7	290.1	McNab and Bonaccorso (2001)
Pteropodidae	*Pteropus poliocephalus*	598	36.5	316.9	McNab and Bonaccorso (2001)
Pteropodidae	*Pteropus pumilus*	194.2	36.1	126.4	McNab and Bonaccorso (2001)
Pteropodidae	*Pteropus rodricensis*	254.5	36.5	134.9	McNab and Bonaccorso (2001)
Pteropodidae	*Pteropus scapulatus*	362	37	242.5	McNab (1969)
Pteropodidae	*Pteropus vampyrus*	1024.3	36.9	804.1	McNab and Bonaccorso (2001)
Pteropodidae	*Rousettus aegyptiacus*	146	34.8	122.6	McNab and Bonaccorso (2001)
Pteropodidae	*Rousettus amplexicaudatus*	91.5	36.5	104.3	McNab and Bonaccorso (2001)
Pteropodidae	*Syconycteris australis*	15.9	35.9	21.9	McNab and Bonaccorso (2001)
Vespertilionidae	*Antrozous pallidus*	22		18.7	Licht and Leitner (1967)
Vespertilionidae	*Chalinolobus gouldii*	17.5	31.1	25.2	Hosken and Withers (1997)
Vespertilionidae	*Eptesicus fuscus*	10.4	36	20.8	Geiser (1988b)
Vespertilionidae	*Histiotus velatus*	11.2	30.5	15.7	McNab (1969)
Vespertilionidae	*Miniopterus gigas*	107.2	35.6	94.3	Baudinette *et al.* (2000)
Vespertilionidae	*Miniopterus schreibersi*	10.91	37.7	26.0	Baudinette *et al.* (2000)
Vespertilionidae	*Myotis lucifuga*	5.2	37	8.9	Geiser (1988b)
Vespertilionidae	*Myotis nigricans*	3.7		4.8	McNab (1989)
Vespertilionidae	*Nyctophilus geoffroyi*	8	31.6	11.2	Hosken and Withers (1999)
Vespertilionidae	*Plecotus auritus*	10.25		12.5	McLean and Speakman (2000)
Hyracoidea (5)		**2215**	**37.4**	**783.19**	
Procaviidae	*Heterohyrax brucei*	2000	36.7	720	McNab (1970)
Procaviidae	*Dendrohyrax dorsalis*	2210		751	Lovegrove (2000)
Procaviidae	*Procavia capensis*	2400	37	660	Rübsamen *et al.* (1979)
Procaviidae	*Procavia habessinica*	2250	38	900	Taylor and Sale (1969)

		M **(g)**	**T_b (°C)**	**BMR (mL O_2 h^{-1})**	**Reference**
Procaviidae	*Procavia johnstoni*	2750	39	1179	Dawson (1973); Heusner (1991)
Insectivora (51)		**54.3**	**35.1**	**60.43**	
Chrysochloridae	*Amblysomus hottentotus*	70		84.7	Lovegrove (2000)
Chrysochloridae	*Chrysochloris asiatica*	44	34.0	51.5	Withers (1978b); Bennett *et al.* (1994)
Chrysochloridae	*Eremitalpa granti namibensis*	20	33.6	10.0	Seymour *et al.* (1998)
Erinaceidae	*Atelerix albiventris*	450	35.2	148.5	McNab (1980)
Erinaceidae	*Echinosorex gymnura*	721.2	36.3	504.8	Whittow *et al.* (1977)
Erinaceidae	*Erinaceus concolor*	822.7	35.2	347.2	Król (1994)
Erinaceidae	*Erinaceus europaeus*	750	34.0	337.5	Shkolnik and Schmidt-Nielsen (1976)
Erinaceidae	*Hemiechinus auritus*	400	33.8	152.0	Shkolnik and Schmidt-Nielsen (1976)
Erinaceidae	*Hylomys suillus*	57.8	37.3	60.1	Genoud and Ruedi (1996); Symonds (1999)
Erinaceidae	*Paraechinus aethiopicus*	450	34.2	112.5	Shkolnik and Schmidt-Nielsen (1976)
Soricidae	*Blarina brevicaudata*	20.5	38.3	65.6	Sparti and Genoud (1989)
Soricidae	*Blarina carolinensis*	10.2	36.8	33.7	Sparti and Genoud (1989)
Soricidae	*Crocidura crossei*	10.2	34.3	22.4	Sparti (1990)
Soricidae	*Crocidura flavescens*	33.2		44.5	Lovegrove (2000)
Soricidae	*Crocidura hildegardeae*	10	35.7	26.0	Sparti (1990)
Soricidae	*Crocidura leucodon*	11.7		29.8	Lovegrove (2000)
Soricidae	*Crocidura luna*	11.8	34.8	24.8	McNab (1979b); Sparti (1990)
Soricidae	*Crocidura olivieri*	38.9	35.3	58.4	McNab (1980); Sparti (1990)
Soricidae	*Crocidura poensis*	17.3	35.5	31.1	Sparti (1990); Król (1994)
Soricidae	*Crocidura russula*	10.4	34.7	22.9	Shkolnik and Schmidt-Nielsen (1976); McNab (1980); Sparti (1990)
Soricidae	*Crocidura suaveolens*	6.5	35.1	18.9	Shkolnik and Schmidt-Nielsen (1976); Sparti (1990)
Soricidae	*Crocidura viaria*	14.7	34.5	22.1	Shkolnik and Schmidt-Nielsen (1976); Sparti (1990)
Soricidae	*Cryptotis parva*	6.2	37	19.2	McNab (1980); Sparti and Genoud (1989)
Soricidae	*Neomys anomalus*	13.1		66.8	Lovegrove (2000)
Soricidae	*Neomys fodiens*	17.1	37.3	54.7	Sparti and Genoud (1989)
Soricidae	*Notiosorex crawfordi*	4	37.6	13.2	Sparti and Genoud (1989)
Soricidae	*Sorex alpinus*	7.9	38.6	48.2	Sparti (1990)
Soricidae	*Sorex araneus*	8.05		60.2	Lovegrove (2000)
Soricidae	*Sorex cinereus*	3.5	38.4	31.5	Sparti and Genoud (1989)
Soricidae	*Sorex coronatus*	9.1	37.6	51.9	Sparti and Genoud (1989)
Soricidae	*Sorex minutus*	4.0	38.5	30.8	Sparti and Genoud (1989)
Soricidae	*Sorex ornatus*	9.7		52.3	Lovegrove (2000)
Soricidae	*Sorex vagrans*	5.2	38	28.1	Sparti and Genoud (1989)
Soricidae	*Suncus etruscus*	2.4	36.0	14.4	Jurgens *et al.* (1996)
Soricidae	*Suncus murinus*	30.2	38.7	59.5	Oron *et al.* (1981); Nicoll and Thompson (1987)
Talpidae	*Condylura cristata*	49	37.7	110.3	Campbell *et al.* (1999); Campbell and Hochachka (2000)
Talpidae	*Neurotrichus gibbsii*	11.8	38.4	46.5	Lovegrove (1989)
Talpidae	*Scalopus aquaticus*	48	36.0	67.7	McNab (1979b)
Talpidae	*Scapanus latimanus*	61		76.2	McNab (1988b)
Talpidae	*Scapanus orarius*	61.2		64.1	Kenagy and Vleck (1982)
Talpidae	*Scapanus townsendii*	130.1		108.9	Kenagy and Vleck (1982)
Tenrecidae	*Echinops telfari*	116.4		133.9	Lovegrove (2000)
Tenrecidae	*Geogale aurita*	6.9	30.8	7.7	Stephenson and Racey (1993b)
Tenrecidae	*Hemicentetes nigriceps*	101.9		72.5	Stephenson and Racey (1994)

		M (g)	T_b (°C)	BMR (mL O_2 h^{-1})	Reference
Tenrecidae	*Hemicentetes semispinosus*	133		64.1	Stephenson and Racey (1994)
Tenrecidae	*Limnogale mergulus*	77.7		55.9	Stevens and Hume (1995)
Tenrecidae	*Microgale cowani*	12.2	33	32.0	Stephenson and Racey (1993b); Symonds (1999)
Tenrecidae	*Microgale dobsoni*	44.6	30.9	56.4	Stephenson and Racey (1993a)
Tenrecidae	*Microgale talazaci*	44	30.8	43.6	Stephenson and Racey (1993a)
Tenrecidae	*Setifer setosus*	530	32.2	121.9	McNab (1980)
Tenrecidae	*Tenrec ecaudatus*	650	33	130.7	Dawson (1973); Stevens and Hume (1995)
Lagomorpha (10)		**420.3**	**39.4**	**427.99**	
Leporidae	*Lepus alleni*	3000	37.9	1650	McNab (1970)
Leporidae	*Lepus americanus*	1581	39.8	1518	McNab (1970)
Leporidae	*Lepus arcticus*	3004.4	38.9	1082	Wang *et al.* (1973)
Leporidae	*Lepus californicus*	2300	39.2	1311	Wang and Hudson (1971)
Leporidae	*Lepus timidus*	3025	39.7	2118	Pyornila *et al.* (1992)
Leporidae	*Lepus townsendii*	2430	38.2	1264	Rogowitz (1990)
Leporidae	*Oryctolagus cuniculus*	2000	39	1140	Hart (1971)
Leporidae	*Sylvilagus audubonii*	672.4	38.3	438	Hinds (1973)
Ochotonidae	*Ochotona princeps*	109	40.1	167	MacArthur and Wang (1973)
Ochotonidae	*Ochotona dauurica*	127.7		249	Weiner and Górecki (1981)
Macroscelidea (8)		**73.9**	**37.0**	**79.26**	
Macroscelididae	*Elephantulus brachyrhynchus*	45.3	37.5	43.7	McNab (1980); Downs and Perrin (1995b)
Macroscelididae	*Elephantulus edwardii*	50	37.6	54.5	McNab (1984)
Macroscelididae	*Elephantulus intufi*	46.49	37.2	52.0	McNab (1980); Downs and Perrin (1995b)
Macroscelididae	*Elephantulus myurus*	62.97	36.9	66.3	Lovegrove *et al.* (2001)
Macroscelididae	*Elephantulus rozeti*	45.31	37.1	47.8	Lovegrove *et al.* (2001)
Macroscelididae	*Elephantulus rufescens*	53	37.3	56.9	McNab (1984)
Macroscelididae	*Macroscelides proboscideus*	39	36.2	52.3	Roxburgh and Perrin (1994)
Macroscelididae	*Petrodromus tetradactylus*	206.11	37.5	179.5	Downs and Perrin (1995b)
Pholidota (5)		**3433**	**32.9**	**565.71**	
Manidae	*Manis crassicaudata*	15910	33.4	1241	McNab (1984)
Manidae	*Manis javanica*	4220	32.3	1106	McNab (1984)
Manidae	*Manis tetradactyla*	1430	33.0	229	Heath and Hammel (1986)
Manidae	*Manis pentadactyla*	3637.5	33.4	668	Heath and Hammel (1986)
Manidae	*Manis tricuspis*	1365	32.6	276	Heath and Hammel (1986)
Primates (25)		**957.4**	**36.4**	**444.24**	
Callitrichidae	*Callithrix jacchus*	190		152	McNab (1988b)
Callitrichidae	*Cebuella pygmaea*	116.8		117	Morrison and Middleton (1967)
Callitrichidae	*Saguinus geoffroyi*	225		234	Scholander *et al.* (1950)
Cebidae	*Alouatta palliata*	4670		2055	Milton and Casey (1979)
Cebidae	*Aotus trivirgatus*	820	38.0	442	Scholander *et al.* (1950)
Cebidae	*Saimiri sciureus*	875	38	801	Robinson *et al.* (1993); Lovegrove (2000)
Cercopithecidae	*Cercopithecus mitis*	8500	37.5	3392	Müller *et al.* (1983)
Cercopithecidae	*Colobus guereza*	10450	37.0	2978	Müller *et al.* (1983)
Cercopithecidae	*Erythrocebus patas*	3000	39.3	1068	Mahoney (1980)
Cercopithecidae	*Papio anubis*	9500	37.3	2778	Heusner (1991)
Cercopithecidae	*Papio ursinus*	16900	37.0	5147	Goldstone *et al.* (1967)
Cheirogaleidae	*Cheirogaleus medius*	300	38.0	195	McCormick (1981)
Indriidae	*Propithecus verreauxi*	3350		670	Ross (1992)
Lemuridae	*Eulemur fulvus*	2330	36.5	746	Daniels (1984)

		M (g)	T_b (°C)	BMR (mL O_2 h^{-1})	Reference
Lorisidae	*Arctocebus calabarensis*	206		131	Lovegrove (2000)
Lorisidae	*Euoticus elegantulus*	261.5		216	Lovegrove (2000)
Lorisidae	*Galago moholi*	170		51	Ross (1992)
Lorisidae	*Galago senegalensis*	171.5	37.9	137	Knox and Wright (1989)
Lorisidae	*Galagoides demidoff*	63.8		59	Lovegrove (2000)
Lorisidae	*Loris tardigradus*	284	35.5	128	Müller *et al.* (1985)
Lorisidae	*Nycticebus coucang*	1160	35.4	273	Müller (1978)
Lorisidae	*Otolemur crassicaudatus*	950		412	Lovegrove (2000)
Lorisidae	*Otolemur garnettii*	1314		704	Ross (1992)
Lorisidae	*Perodicticus potto*	964	36.1	327	Hildwein and Goffart (1975)
Tarsiidae	*Tarsius syrichta*	113	33.8	77	McNab and Wright (1987)
Tarsiidae	*Tarsius spectrum*	173		149	Clarke (1943)
Rodentia (289)		**580.7**	**36.7**	**325.07**	
Agoutidae	*Agouti paca*	9156	37.2	2746.8	Arends and McNab (2001)
Aplodontidae	*Aplodontia rufa*	630	38.0	277.2	McNab (1979b)
Bathyergidae	*Bathyergus janetta*	406	34.7	215.2	Lovegrove (1986b)
Bathyergidae	*Bathyergus suillus*	620	35.3	303.8	Lovegrove (1986b)
Bathyergidae	*Cryptomys bocagei*	94	33.7	69.6	Bennett *et al.* (1994)
Bathyergidae	*Cryptomys damarensis*	138	35.2	78.7	Lovegrove (1986a); Lovegrove and Wissel (1988); Bennett *et al.* (1992)
Bathyergidae	*Cryptomys darlingi*	60	33.3	58.8	Bennett *et al.* (1993)
Bathyergidae	*Cryptomys hottentotus*	75	34.4	67.5	Bennett *et al.* (1992)
Bathyergidae	*Cryptomys hottentotus amatus*	79.5	35.0	55.5	Bennett *et al.* (1994); Marhold and Nagel (1995)
Bathyergidae	*Cryptomys hottentotus natalensis*	102		81.6	Lovegrove (2000)
Bathyergidae	*Cryptomys mechowi*	267	34.0	160.2	Bennett *et al.* (1994)
Bathyergidae	*Georychus capensis*	195	36.4	115.7	Du Toit *et al.* (1985); Lovegrove (1987)
Bathyergidae	*Heliophobius argentocinereus*	88	35.1	74.8	McNab (1979a)
Bathyergidae	*Heterocephalus glaber*	32	32.1	20.5	McNab (1966b); Withers and Jarvis (1980)
Capromyidae	*Capromys pilorides*	2630	35.7	604.9	Arends and McNab (2001)
Capromyidae	*Geocapromys ingrahami*	775		265.8	Arends and McNab (2001)
Capromyidae	*Geocapromys brownii*	2456		736.8	Arends and McNab (2001)
Caviidae	*Cavia porcellus*	629	39	346.0	Arends and McNab (2001)
Caviidae	*Dolichotis salinicola*	1613	38.4	725.9	Arends and McNab (2001)
Caviidae	*Galea musteloides*	322	37.3	264.0	Arends and McNab (2001)
Caviidae	*Kerodon ruprestris*	801	38.2	360.5	Arends and McNab (2001)
Caviidae	*Microcavia niata*	255		175.7	Lovegrove (2000)
Chinchillidae	*Chinchilla laniger*	426	35.7	200.2	Arends and McNab (2001)
Chinchillidae	*Lagostomus maximus*	6784	36.8	1899.5	Arends and McNab (2001)
Ctenomyidae	*Ctenomys australis*	340	37.3	116.6	Busch (1989)
Ctenomyidae	*Ctenomys fulvus*	300	36.2	189.0	McNab (1988a); Cortés *et al.* (2000)
Ctenomyidae	*Ctenomys maulinus*	215	36.2	187.1	Arends and McNab (2001)
Ctenomyidae	*Ctenomys opimus*	214	36	109.7	Arends and McNab (2001)
Ctenomyidae	*Ctenomys peruanus*	490	35.2	220.5	Arends and McNab (2001)
Ctenomyidae	*Ctenomys talarum*	121	36.1	109.6	Busch (1989)
Dasyproctidae	*Dasyprocta azarae*	3849	37.5	1886.0	Arends and McNab (2001)
Dasyproctidae	*Dasyprocta leporina*	2687	38.3	1558.5	Arends and McNab (2001)
Dasyproctidae	*Myoprocta acouchy*	914	35.4	502.7	Arends and McNab (2001)
Dipodidae	*Dipus sagitta?*	160	36.8	121.2	Hart (1971); Heusner (1991)

		M (g)	T_b (°C)	**BMR** (mL O_2 h^{-1})	**Reference**
Dipodidae	*Jaculus jaculus*	75	37.5	92.3	Hooper and Hilali (1972)
Dipodidae	*Jaculus orientalis*	139	37	139.0	Hooper and Hilali (1972)
Dipodidae	*Napaeozapus insignis*	22	37	39.6	Brower and Cade (1966)
Dipodidae	*Sicista betulina*	10		32.0	Lovegrove (2000)
Dipodidae	*Zapus hudsonicus*	23.8	37.3	35.7	Geiser (1988b)
Echimyidae	*Proechimys semispinosus*	498	37.9	313.7	Arends and McNab (2001)
Echimyidae	*Thrichomys apereoides*	323	37.6	206.7	Arends and McNab (2001)
Erethizontidae	*Coendou prehensilis*	3280	36.7	918.4	Arends and McNab (2001)
Erethizontidae	*Erethizon dorsatum*	11136		2784.0	Arends and McNab (2001)
Geomyidae	*Geomys bursaris*	197	35.0	137.9	Bradley and Yousef (1975)
Geomyidae	*Geomys pinetis*	173	36.3	133.2	McNab (1966b)
Geomyidae	*Thomomys bottae*	143	36.0	120.1	Vleck (1979)
Geomyidae	*Thomomys talpoides*	106.8	36.2	142.0	Bradley *et al.* (1974); Gettinger (1975)
Geomyidae	*Thomomys umbrinus*	85	34.6	72.3	Bradley *et al.* (1974)
Heteromyidae	*Chaetodipus baileyi*	29.1	32.5	34.5	Hinds and MacMillen (1985)
Heteromyidae	*Chaetodipus californicus*	22	38.0	21.3	Tucker (1965)
Heteromyidae	*Chaetodipus fallax*	19.6	32.6	26.9	Hinds and MacMillen (1985)
Heteromyidae	*Chaetodipus hispidus*	39.5	36.8	49.4	Wang and Hudson (1970)
Heteromyidae	*Chaetodipus intermedius*	15.0	36.0	17.9	Bradley *et al.* (1974)
Heteromyidae	*Chaetodipus penicillatus*	16		22.4	Brower and Cade (1966)
Heteromyidae	*Dipodomys agilis*	60.6	37.0	63.6	Carpenter (1966)
Heteromyidae	*Dipodomys deserti*	106	36.8	92.2	Arends and McNab (2001)
Heteromyidae	*Dipodomys heermanni*	63.3		73.2	Hinds and Rice-Warner (1992)
Heteromyidae	*Dipodomys merriami*	36.5	37.0	42.5	Dawson (1955); Carpenter (1966)
Heteromyidae	*Dipodomys microps*	57.2	35.0	66.9	Breyen *et al.* (1973)
Heteromyidae	*Dipodomys nitratoides*	37.8		46.1	Hinds and Rice-Warner (1992)
Heteromyidae	*Dipodomys ordii*	46.8	34.6	64.2	Hinds and MacMillen (1985)
Heteromyidae	*Dipodomys panamintinus*	64.2	36.9	74.3	Hart (1971); Hinds and MacMillen (1985)
Heteromyidae	*Heteromys anomalus*	69.3	36.0	100.5	Arends and McNab (2001)
Heteromyidae	*Heteromys desmarestianus*	75.8	33.8	99.1	Hinds and MacMillen (1985)
Heteromyidae	*Liomys irroratus*	48.1	37.0	53.9	Hudson and Rummel (1966a)
Heteromyidae	*Liomys salvani*	43.8	37.0	46.9	Hudson and Rummel (1966a)
Heteromyidae	*Microdipodops megacephalus*	11	32.8	30.2	Hinds and MacMillen (1985)
Heteromyidae	*Microdipodops pallidus*	15.2	39.3	19.8	Bartholomew and MacMillen (1960)
Heteromyidae	*Perognathus flavus*	8.3	34.6	17.3	Hinds and MacMillen (1985)
Heteromyidae	*Perognathus longimembris*	8.9	34.7	9.5	Chew *et al.* (1967)
Hydrochaeridae	*Hydrochaeris hydrochaeris*	26385	37.1	6596.3	Arends and McNab (2001)
Hystricidae	*Hystrix africaeaustralis*	11300	37.5	2361.7	Haim *et al.* (1990)
Muridae	*Abrothrix lanosus*	24		45.6	Bozinovic (1992)
Muridae	*Abrothrix longipilis*	42.3	37.4	57.5	Bozinovic and Rosenmann (1988)
Muridae	*Acomys cahirinus*	42	37.5	46.2	Shkolnik and Borut (1969)
Muridae	*Acomys russatus*	55.55	37.3	42.9	Shkolnik and Borut (1969); Haim (1987)
Muridae	*Acomys spinosissimus*	27.02		44.1	Perrin and Downs (1994)
Muridae	*Acomys subspinosus*	32.25		83.4	Perrin and Downs (1994)
Muridae	*Aethomys namaquensis*	64.2	36.8	56.8	Lovegrove *et al.* (1991)
Muridae	*Akodon albiventer*	31		46.5	Bozinovic (1992)
Muridae	*Akodon azarae*	24	37.7	40.8	Bozinovic and Rosenmann (1988)
Muridae	*Alticola argentatus*	37.7		121.0	Weiner and Górecki (1981)
Muridae	*Apodemus flavicollis*	23.9	36.7	43.3	Haim and Izhaki (1995)

		M (g)	***T_b*** (°C)	**BMR** (mL O_2 h^{-1})	**Reference**
Muridae	*Apodemus hermonensis*	20.5	37	50.0	Haim and Izhaki (1995)
Muridae	*Apodemus mystacinus*	40.4	35.5	56.0	Haim (1987); Haim and Izhaki (1993)
Muridae	*Apodemus sylvaticus*	23.9	36.7	43.3	Haim (1987); Haim and Izhaki (1993)
Muridae	*Arborimus longicaudus*	21.8	37.3	58.9	McNab (1992b)
Muridae	*Arvicola terrestris*	92.0	37.5	106.7	McNab (1992b)
Muridae	*Auliscomys micropus*	62.3	37.4	97.8	Bozinovic and Rosenmann (1988)
Muridae	*Baiomys taylori*	7.15	36	17.1	Hart (1971); Lovegrove (2000)
Muridae	*Calomys ducilla?*	16		28.8	Rosenmann and Morrison (1974)
Muridae	*Calomys musculinus*	16.9	36.2	27.6	Bozinovic and Rosenmann (1988)
Muridae	*Calomys venustus*	50.1	37.1	74.7	Bozinovic and Rosenmann (1988); Caviedes-Vidal *et al.* (1990)
Muridae	*Cannomys badius*	344	36.0	172.0	McNab (1979b)
Muridae	*Chelemys macronyx*	62	36.8	84.3	Bozinovic and Rosenmann (1988)
Muridae	*Chionomys nivalis*	32.8		81.0	Lovegrove (2000)
Muridae	*Chroeomys anadinus*	34.6	37.7	64.7	Bozinovic and Rosenmann (1988)
Muridae	*Chroeomys olivaceus*	27	37.2	49.4	Bozinovic and Rosenmann (1988)
Muridae	*Cleithrionomys glareolus*	23.4		63.4	Lovegrove (2000)
Muridae	*Cleithrionomys rufocanus*	27		59.4	McNab (1992a)
Muridae	*Cleithrionomys rutilus*	28		77.0	Rosenmann *et al.* (1975)
Muridae	*Clethrionomys califomicus*	18.3	37.5	61.1	McNab (1992a)
Muridae	*Clethrionomys gapperi*	22.3	37.9	49.3	McNab (1992a)
Muridae	*Conilurus penicillatus*	213.2		162.7	Hinds and Rice-Warner (1992)
Muridae	*Cricetomys gambianus*	1870	35.6	1140.7	Knight (1988)
Muridae	*Cricetulus migratorius*	30.7	38.1	43.9	Haim and Izhaki (1993)
Muridae	*Cricetus cricetus*	362	39.5	231.7	Hart (1971); Lovegrove (2000)
Muridae	*Desmodillus auricularis*	71.93	35.9	87.8	Downs and Perrin (1994)
Muridae	*Dicrostonyx groenlandicus*	59.62	38.4	98.8	McNab (1992a)
Muridae	*Eligmodontia typus*	17.5	36.4	29.9	Bozinovic and Rosenmann (1988)
Muridae	*Euneomys chinchilloides*	65.4		84.4	Bozinovic (1992)
Muridae	*Gerbillurus paeba*	33.9	38.7	34.8	Downs and Perrin (1990)
Muridae	*Gerbillurus setzeri*	46.1	37.6	37.0	Downs and Perrin (1990)
Muridae	*Gerbillurus tytonis*	29.9	36.9	31.7	Downs and Perrin (1990)
Muridae	*Gerbillurus vallinus*	38.8	37.4	34.8	Downs and Perrin (1990)
Muridae	*Gerbillus allenybi*	35.3	36.3	38.8	Haim (1984)
Muridae	*Gerbillus dasyurus*	27.6	38.6	29.3	Haim (1987)
Muridae	*Gerbillus gerbillus*	29.7	37.2	42.5	Haim and Izhaki (1993)
Muridae	*Gerbillus nanus*	28.4	38.8	22.2	Haim and Izhaki (1993)
Muridae	*Gerbillus perpallidus*	52.4		43.5	Lovegrove (2000)
Muridae	*Gerbillus pusillus*	12.6	34.6	13.5	Buffenstein and Jarvis (1985)
Muridae	*Gerbillus pyramidum*	108.5	36.1	81.4	Robinson and Hendrickson (1961)
Muridae	*Graomys griseoflavus*	69.4	36.1	84.0	Bozinovic and Rosenmann (1988)
Muridae	*Hydromys chrysogaster*	900	36.6	528.3	Dawson and Fanning (1981)
Muridae	*Isthmomys pirrensis*	137.9	37.6	121.4	Hill (1975)
Muridae	*Lagurus curtatus*	30.3	37.1	50.3	McNab (1992a)
Muridae	*Lemmus lemmus*	80	37.8	192.0	Hissa (1970)
Muridae	*Lemmus sibericus*	50.2	38.3	90.2	McNab (1992a)
Muridae	*Lemniscomys griselda*	47.5	36.9	57.6	Haim (1987)
Muridae	*Lemniscomys rosalia*	50.53	36.5	61.5	Haim (1981)
Muridae	*Malacothrix typica*	21.7	37.0	20.6	Knight and Skinner (1981)

		M (g)	**T_b** (°C)	**BMR** (mL O_2 h^{-1})	**Reference**
Muridae	*Maresomys boliviensis*	76.8	36.3	110.6	Bozinovic and Rosenmann (1988)
Muridae	*Mastomys natalensis*	41.5	38.0	32.8	Haim and Fourie (1980)
Muridae	*Megadontomys thomasi*	110.8	37.8	124.1	Hart (1971); Lovegrove (2000)
Muridae	*Meriones hurriane*	69	36.1	54.5	Goyal *et al.* (1981)
Muridae	*Meriones tristrami*	112	36.5	98.6	Haim and Izhaki (1993)
Muridae	*Meriones unguiculatus*	67	38.2	77.1	Weiner and Górecki (1981)
Muridae	*Mesocricetus auratus*	98	38.1	147.0	Hart (1971)
Muridae	*Micromys minutus*	7.37	38	21.1	Hart (1971); Lovegrove (2000)
Muridae	*Microtus agrestis*	28	37.6	63.6	McDevitt and Speakman (1996)
Muridae	*Microtus arvalis*	20	37	62.0	Ishii *et al.* (1996); Lovegrove (2000)
Muridae	*Microtus brandti*	40.2	36.2	76.8	Weiner and Górecki (1981); Li *et al.* (2001)
Muridae	*Microtus breweri*	53.1	37.3	73.8	Kurta and Ferkin (1991)
Muridae	*Microtus californicus*	44	38.8	68.2	McNab (1992a)
Muridae	*Microtus guentheri*	43.8	38.3	80.2	Haim and Izhaki (1993)
Muridae	*Microtus longicaudus*	28.6	38	67.5	McNab (1992a)
Muridae	*Microtus mexicanus*	28.8	37.9	46.9	McNab (1992a)
Muridae	*Microtus montanus*	35.1	35.3	83.3	McNab (1992a)
Muridae	*Microtus ochrogaster*	46.7	37.9	79.1	McNab (1992a)
Muridae	*Microtus oeconomus*	33.7	38.4	100.9	McNab (1992a)
Muridae	*Microtus pennsylvanicus*	38.9	38.5	75.1	McNab (1992a)
Muridae	*Microtus pinetorum*	25.5	38.3	58.4	McNab (1992a)
Muridae	*Microtus richardsoni*	65.65	38.7	128.0	McNab (1992a)
Muridae	*Microtus subterraneus*	17.8		49.5	Lovegrove (2000)
Muridae	*Microtus townsendii*	52.2		90.4	Kenagy and Vleck (1982)
Muridae	*Microtus xanthognathus*	68.5	38	98.6	McNab (1992a)
Muridae	*Millardia meltada*	67.4		58.6	Lovegrove (2000)
Muridae	*Mus minutoides*	8.06	36.3	24.0	Downs and Perrin (1996)
Muridae	*Mus spretus*	21.8		61.9	Lovegrove (2000)
Muridae	*Myopus schisticolor*	26.4	39.0	93.5	Saarela and Hissa (1993)
Muridae	*Mystromys albicaudatus*	93.78	33	126.8	Downs and Perrin (1995a)
Muridae	*Nannospalax ehrenbergi* (2n = 52)	138	34.9	118.7	Nevo and Shkolnik (1974); Haim and Izhaki (1993)
Muridae	*Nannospalax ehrenbergi* (2n = 54)	134	35.8	101.8	Nevo and Shkolnik (1974); Haim and Izhaki (1993)
Muridae	*Nannospalax ehrenbergi* (2n = 58)	135	36.0	114.8	Nevo and Shkolnik (1974); Haim and Izhaki (1993)
Muridae	*Nannospalax ehrenbergi* (2n = 60)	134	35.5	82.8	Nevo and Shkolnik (1974); Haim and Izhaki (1993)
Muridae	*Nannospalax leucodon*	201	36.3	148.7	McNab (1979b)
Muridae	*Neofiber alleni*	258.1	37.1	216.8	McNab (1992a)
Muridae	*Neotoma albigula*	183		134.5	McNab (1986)
Muridae	*Neotoma cinerea*	205.1		168.6	McNab (1986)
Muridae	*Neotoma fuscipes*	187	36.6	147.7	McNab (1970)
Muridae	*Neotoma lepida*	110	36.8	86.9	McNab (1970)
Muridae	*Notomys alexis*	32.3	38.0	45.2	MacMillen and Lee (1970)
Muridae	*Notomys cervinus*	34.2	38.5	41.7	MacMillen and Lee (1970)
Muridae	*Ochrotomys nuttalli*	19.5	36.4	27.1	Layne and Dolan (1975)
Muridae	*Oligoryzomys longicaudatus*	28.2	37.3	51.0	Bozinovic and Rosenmann (1988)
Muridae	*Ondatra zibethicus*	1004.6	37.4	642.9	McNab (1992a)
Muridae	*Onychomys torridus*	19.1		29.6	Whitford and Conley (1971)

		M (g)	**T_b** (°C)	**BMR** (mL O_2 h^{-1})	**Reference**
Muridae	*Otomys irroratus*	102	37.6	84.9	Haim (1987)
Muridae	*Otomys sloggetti*	113.29	38	133.7	Richter *et al.* (1997)
Muridae	*Otomys unisulcatus*	96	34.8	106.6	Du Plessis *et al.* (1989)
Muridae	*Oxymycterus roberti*	83.5	38.3	91.0	McNab (1984)
Muridae	*Parotomys brantsii*	86.5	35.1	83.9	Du Plessis *et al.* (1989)
Muridae	*Peromyscus boylii*	23.2		54.3	Mazen and Rudd (1980)
Muridae	*Peromyscus californicus*	47.6	36.4	52.4	McNab and Morrison (1963); Tucker (1965)
Muridae	*Peromyscus c. insignis*	45.5	36.0	45.5	Hart (1971)
Muridae	*Peromyscus c. parasiticus*	49.6	36.4	58.0	McNab and Morrison (1963)
Muridae	*Peromyscus crinitus*	15.9	35.7	25.1	McNab and Morrison (1963)
Muridae	*Peromyscus eremicus*	21.5	36.6	33.1	McNab and Morrison (1963)
Muridae	*Peromyscus gossypinus*	21.5	37.5	37.0	Glenn (1970); Tannenbaum and Pivorun (1988)
Muridae	*Peromyscus leucopus*	20	36.7	33.2	Geiser (1988b)
Muridae	*Peromyscus l. noveboracensis*	26	37.5	57.2	Hart (1971); Tannenbaum and Pivorun (1988)
Muridae	*Peromyscus maniculatus*	22.8	36.6	36.9	McNab and Morrison (1963); Tomasi (1985)
Muridae	*Peromyscus m.artemisidae*	23.19	37.2	46.1	Hayward (1965)
Muridae	*Peromyscus m. austerus*	19.53	36.3	39.8	Hayward (1965)
Muridae	*Peromyscus m. gambeli*	19.1	36.8	39.0	McNab and Morrison (1963)
Muridae	*Peromyscus m. nebrascensis*	18.93	35.9	39.4	Hayward (1965)
Muridae	*Peromyscus m. sonoriensis*	20.38	36.7	37.5	Hayward (1965)
Muridae	*Peromyscus megalops*	66.2		90.7	McNab (1988a)
Muridae	*Peromyscus oreas*	24.58	36.2	43.5	Hayward (1965)
Muridae	*Peromyscus polionotus*	12		21.5	Glenn (1970)
Muridae	*Peromyscus sitkensis*	28.3	36.0	46.7	Hayward (1965)
Muridae	*Peromyscus truei gilberti*	33.3	36.4	62.6	McNab and Morrison (1963)
Muridae	*Peromyscus truei truei*	33.2	36.7	50.8	McNab and Morrison (1963)
Muridae	*Phenacomys intermedius*	21.5	37.9	67.3	McNab (1992a)
Muridae	*Phodopus sungorus*	25.7	36.1	40.9	Weiner and Heldmaier (1987)
Muridae	*Phyllotis darwini chilensis*	49		65.7	Bozinovic (1992)
Muridae	*Phyllotis darwini darwini*	59	36.2	71.4	Bozinovic and Rosenmann (1988)
Muridae	*Phyllotis darwini rupestris*	36	37.1	45.4	Bozinovic (1992)
Muridae	*Phyllotis magister*	62.8		69.0	Rezende *et al.* (2001)
Muridae	*Phyllotis xanthopygus*	55	37.3	56.7	Bozinovic and Rosenmann (1988)
Muridae	*Podomys floridanus*	30.8		51.7	Glenn (1970)
Muridae	*Pseudomys gracilicaudatus*	79.8	36.8	83.8	Dawson and Dawson (1981)
Muridae	*Pseudomys hermannsburgensis*	12.2	37.8	23.3	MacMillen *et al.* (1972)
Muridae	*Rattus colletti*	165.7		123.0	Hinds and Rice-Warner (1992)
Muridae	*Rattus fuscipes*	76	37.5	84.4	Collins (1973a)
Muridae	*Rattus lutreolis*	109	36.7	63.2	Collins (1973b)
Muridae	*Rattus sordidus*	187		106.6	Collins and Bradshaw (1973)
Muridae	*Rattus villosissimus*	250.6	35.9	145.8	Hinds and Rice-Warner (1992)
Muridae	*Reithrodon auritus*	78.7		76.8	Bozinovic (1992)
Muridae	*Reithrodontomys megalotis*	9.0	36.8	22.5	Pearson (1960); Tomasi (1985)
Muridae	*Rhabdomys pumilio*	39.6	37	32.1	Haim (1987)
Muridae	*Saccostomus campestris*	61.3	35.3	51.5	Haim *et al.* (1991)
Muridae	*Scotinomys teguina*	12	37.6	31.2	Hill and Hooper (1971)
Muridae	*Scotinomys xerampelinus*	15.2	36.2	31.9	Hill and Hooper (1971)
Muridae	*Sekeetamys calurus*	56.9	37.5	44.4	Haim and Skinner (1991)

		M (g)	T_b (°C)	BMR (mL O_2 h^{-1})	Reference
Muridae	*Sigmodon alleni*	137.8		203.3	Bowers (1971)
Muridae	*Sigmodon fulviventer*	137.8		207.4	Bowers (1971)
Muridae	*Sigmodon hispidus*	139.3	38.1	230.4	Bowers (1971); Scheck (1982)
Muridae	*Sigmodon leucotis*	128.6		186.5	Bowers (1971)
Muridae	*Sigmodon ochrognathus*	115.1		154.2	Bowers (1971)
Muridae	*Steatomys pratensis*	37.54	34.1	18.8	Ellison (1995); Lovegrove (2000)
Muridae	*Stochomys longicaudatus*	84.2		97.5	Lovegrove (2000)
Muridae	*Tachyoryctes splendens*	191	35.9	150.9	McNab (1979b)
Muridae	*Tatera afra*	106.5	34	182.1	Duxbury and Perrin (1992)
Muridae	*Tatera indica*	87		75.7	Goyal *et al.* (1981)
Muridae	*Tatera leucogaster*	157.62	35.1	132.6	Downs and Perrin (1994)
Muridae	*Thallomys paedulcus*	132.4	36.7	87.3	Lovegrove *et al.* (1991)
Muridae	*Uromys caudimaculatus*	812		570.8	Hinds and Rice-Warner (1992)
Myoxidae	*Myoxus glis*	200	37.7	158.0	Geiser (1988b)
Myoxidae	*Muscardenis avellanarius*	23.5	35.8	63.0	Geiser (1988b)
Myoxidae	*Graphiurus ocularis*	67.8		66.4	Lovegrove (2000)
Octodontidae	*Aconaemys fuscus*	112	37.3	121.0	McNab (1988a)
Octodontidae	*Octodon bridgesi*	176.1		183.3	Bozinovic (1992)
Octodontidae	*Octodon degus*	193.0	37.6	170.2	Bozinovic and Novoa (1997); Arends and McNab (2001)
Octodontidae	*Octodon lunatus*	173.2		171.5	Bozinovic (1992)
Octodontidae	*Octodontomys gliroides*	152	37.2	130.7	Arends and McNab (2001)
Octodontidae	*Octomys mimax*	118.6	36.7	115.0	Bozinovic and Contreras (1990)
Octodontidae	*Spalacopus cyanus*	135	36.5	106.8	McNab (1979a); Contreras (1986); Arends and McNab (2001)
Octodontidae	*Tympanoctomys barrerae*	71.4	35.7	77.1	Bozinovic and Contreras (1990)
Peditidae	*Pedetes capensis*	2300	35.9	793.5	Lovegrove (2000)
Sciuridae	*Ammospermophilus leucurus*	95.7	37.5	93.9	Chappell and Bartholomew (1981a); Chappell and Bartholomew (1981b); Lovegrove (2000)
Sciuridae	*Cynomys ludovicanus*	1112.3	36.7	422.7	Reinking *et al.* (1977)
Sciuridae	*Epixerus wilsoni*	460		241.5	Lovegrove (2000)
Sciuridae	*Funisciurus congicus*	112.3	39.3	95.5	Viljoen (1985)
Sciuridae	*Funisciurus isabella*	60		102.1	Lovegrove (2000)
Sciuridae	*Funisciurus lemnisciatus*	95		89.6	Lovegrove (2000)
Sciuridae	*Funisciurus pyrrhopus*	244		181.3	Lovegrove (2000)
Sciuridae	*Glaucomys volans*	64.25	39	67.5	Stapp (1992)
Sciuridae	*Heliosciurus rufobrachium*	230		133.4	Lovegrove (2000)
Sciuridae	*Marmota flaviventris*	4295	36.5	1546.2	Reinking *et al.* (1977)
Sciuridae	*Marmota monax*	2650	37	662.5	Benedict (1938)
Sciuridae	*Paraxerus cepapi*	223.6	39.1	145.3	Viljoen (1985)
Sciuridae	*Paraxerus palliatus ornatus*	366.6	39.3	260.3	Viljoen (1985)
Sciuridae	*Paraxerus palliatus tongensis*	206	38.8	175.1	Viljoen (1985)
Sciuridae	*Sciurus aberti*	624	40.7	430.6	Golightly and Ohmart (1978)
Sciuridae	*Sciurus carolinensis*	440	38.7	369.6	Bolls and Perfect (1972)
Sciuridae	*Spermophilus armatus*	320	35.7	147.2	Hudson *et al.* (1972)
Sciuridae	*Spermophilus beecheyi*	599.6	37.6	317.8	Baudinette (1972)
Sciuridae	*Spermophilus beldingi*	303	35.5	127.3	Hudson *et al.* (1972)
Sciuridae	*Spermophilus citellus*	240	37.5	228.0	Hart (1971)
Sciuridae	*Spermophilus lateralis*	237	36.3	143.4	Hudson *et al.* (1972); Geiser (1988b)

		M (g)	T_b (°C)	BMR (mL O_2 h^{-1})	Reference
Sciuridae	*Spermophilus mohavensis*	240	37.0	112.8	Hudson *et al.* (1972)
Sciuridae	*Spermophilus parryi*	650	37	520.0	Geiser (1988b)
Sciuridae	*Spermophilus richardsoni*	274	35.5	131.5	Hudson *et al.* (1972)
Sciuridae	*Spermophilus satutatus*	252.2		161.4	Kenagy and Vleck (1982)
Sciuridae	*Spermophilus spilosoma*	174	36.1	92.2	Hudson *et al.* (1972)
Sciuridae	*Spermophilus tereticaudus*	167	36.3	93.5	Hudson *et al.* (1972)
Sciuridae	*Spermophilus townsendii*	229	35.6	105.3	Hudson *et al.* (1972)
Sciuridae	*Spermophilus tridecemlineatus*	205.4	35.7	140.4	Hudson *et al.* (1972); Maclean (1981)
Sciuridae	*Spermophilus undulatus*	680	38	667.1	Casey *et al.* (1979)
Sciuridae	*Tamias alpinus*	39		57.7	McNab (1986)
Sciuridae	*Tamias amoenus*	57.1	37	96.3	Jones and Wang (1976); Kenagy and Vleck (1982)
Sciuridae	*Tamias merriami*	75	37	78.8	Wunder (1970)
Sciuridae	*Tamias minimus*	45.8	37	72.7	Willems and Armitage (1975); Jones and Wang (1976)
Sciuridae	*Tamias palmeri*	69.4		113.1	Yousef *et al.* (1974)
Sciuridae	*Tamias striatus*	87.4	38.2	90.0	Wang and Hudson (1971)
Sciuridae	*Tamiasciurus hudsonicus*	228.3	38.7	254.6	Pauls (1981)
Sciuridae	*Tamiasciurus hudsonicus preblei*	202		323.2	Irving *et al.* (1955)
Sciuridae	*Xerus inauris*	542	36.8	326.3	Haim *et al.* (1987)
Sciuridae	*Xerus princeps*	602	37.6	340.1	Haim *et al.* (1987)
Scandentia (3)		**123.0**	**36.8**	**96.95**	
Tupaiidae	*Ptilocerus lowii*	58	36.5	43.5	Whittow and Gould (1976)
Tupaiidae	*Tupaia glis*	123	37	93.5	Bradley and Hudson (1974)
Tupaiidae	*Urogale everetti*	260.6		224.1	Nelson and Asling (1962)
Tublidentata					
Orycteropodidae	*Orycteropus afer*	48000	34.5	6144	McNab (1984)
Xenarthra (15)		**3679**	**33.6**	**670.39**	
Bradypodidae	*Bradypus variegatus*	3790	33	686	McNab (1978)
Dasypodidae	*Cabassous centralis*	4330	33.6	917	McNab (1980)
Dasypodidae	*Chaetophractus nationi*	2150	35.5	559	McNab (1980)
Dasypodidae	*Chaetophractus vellerosus*	1110	34.4	306	McNab (1980)
Dasypodidae	*Chaetophractus villosus*	4540	35.1	808	McNab (1980)
Dasypodidae	*Dasypus novemcinctus*	3510	34.5	865	McNab (1980)
Dasypodidae	*Euphractus sexcinctus*	8190	34.2	1237	McNab (1980)
Dasypodidae	*Priodontes maximus*	45190	33.6	3028	McNab (1980)
Dasypodidae	*Tolypeutes matacus*	1160	33.0	210	McNab (1980)
Dasypodidae	*Zaedyus pichi*	1740	35.2	393	McNab (1980)
Megalonychidae	*Choloepus hoffmanni*	3770	34.4	603	McNab (1970)
Myrmecophagidae	*Cyclopes didactylus*	240	33	114	McNab (1984)
Myrmecophagidae	*Myrmecophaga tridactyla*	30600	32.5	2607	Heath and Hammel (1986)
Myrmecophagidae	*Tamandua mexicana*	3977	32	992	McNab (1984)
Myrmecophagidae	*Tamandua tetradactyla*	3500	33.5	899	Heath and Hammel (1986)
Dasyuromorpha (23)		**177.9**	**34.0**	**91.51**	
Dasyuridae	*Antechinomys laniger*	25.8	35.8	25.3	Withers *et al.* (2000)
Dasyuridae	*Antechinomys laniger 'spenceri'*	24.2		23.7	Withers *et al.* (2000)

		M (g)	T_b (°C)	BMR (mL O_2 h^{-1})	**Reference**
Dasyuridae	*Antechinus flavipes*	46.5	35	45.1	Geiser (1988a)
Dasyuridae	*Antechinus stuartii*	28.2	35.1	33.8	Withers *et al.* (2000)
Dasyuridae	*Antechinus swainsoni*	66.9	36.0	63.0	Chappell and Dawson (1994)
Dasyuridae	*Dasycercus cristicaudata*	101	36.9	51.0	Withers *et al.* (2000)
Dasyuridae	*Dasyuroides byrnei*	91.7	35.2	71.7	Withers *et al.* (2000)
Dasyuridae	*Dasyurus geoffroyi*	1354	36.2	568.7	Withers *et al.* (2000)
Dasyuridae	*Dasyurus hallucatus*	558	35.9	243.0	Withers *et al.* (2000)
Dasyuridae	*Dasyurus maculatus*	1782	36.9	588.1	Withers *et al.* (2000)
Dasyuridae	*Dasyurus viverrinus*	982	35.9	396.2	Withers *et al.* (2000)
Dasyuridae	*Ningaui yvonnae*	11.6	34.4	15.7	Withers *et al.* (2000)
Dasyuridae	*Phascogale tapoatafa*	157	37.4	127.2	Withers *et al.* (2000)
Dasyuridae	*Planigale gilesi*	9.1	35.1	7.0	Withers *et al.* (2000)
Dasyuridae	*Planigale ingrami*	7.1		11.3	Lovegrove (2000)
Dasyuridae	*Planigale maculata*	10.8	34.5	12.0	Withers *et al.* (2000)
Dasyuridae	*Planigale tenuirostris*	7.1	34.5	11.3	Withers *et al.* (2000)
Dasyuridae	*Pseudantechinus macdonnellensis*	43.1	34.2	27.2	Withers *et al.* (2000)
Dasyuridae	*Sarcophilus harrisii*	5775	35.8	1325.4	Withers *et al.* (2000)
Dasyuridae	*Sminthopsis crassicaudata*	16.4	35.2	25.1	Withers *et al.* (2000)
Dasyuridae	*Sminthopsis macroura*	19.35	33.3	22.5	Withers *et al.* (2000)
Dasyuridae	*Sminthopsis murina*	19	35	21.5	Withers *et al.* (2000)
Myrmecobiidae	*Myrmecobius fasciatus*	400	32.5	142.4	Withers *et al.* (2000)
Didelphimorphia (11)		**300.1**	**34.9**	**191.37**	
Caluromyidae	*Caluromys derbianus*	329	35	225	Chappell and Dawson (1994); Withers *et al.* (2000)
Didelphidae	*Chironectes minimus*	935	35	457	Withers *et al.* (2000)
Didelphidae	*Didelphis marsupialis*	1165	35	571	Withers *et al.* (2000)
Didelphidae	*Didelphis virginiana*	2488	35	832	Withers *et al.* (2000)
Didelphidae	*Lutreolina crassicaudata*	812	35.8	406	Withers *et al.* (2000)
Didelphidae	*Philander opossum*	751	35.8	338	Withers *et al.* (2000)
Marmosidae	*Gracilinanus microtarsus*	13	35	19	Withers *et al.* (2000)
Marmosidae	*Marmosa robinsoni*	122	34	98	Withers *et al.* (2000)
Marmosidae	*Metachirus nudicaudatus*	336	35	205	Withers *et al.* (2000)
Marmosidae	*Monodelphis brevicaudata*	75.5	33.7	57	Withers *et al.* (2000)
Marmosidae	*Monodelphis domestica*	104	32.6	60	Withers *et al.* (2000)
Diprotodontia (25)		**544.1**	**35.8**	**265.06**	
Acrobatidae	*Acrobates pygmaeus*	14	34.7	15.1	Withers *et al.* (2000)
Burramyidae	*Burramys parvus*	44.3	36.1	36.8	Hulbert and Dawson (1974); Withers *et al.* (2000)
Burramyidae	*Cercartetus conncinnus*	18.6	34.4	22.3	Geiser (1988b)
Burramyidae	*Cercartetus lepidus*	12.6	33.7	18.8	Geiser (1988b)
Burramyidae	*Cercartetus nanus*	70	35.6	60.2	Withers *et al.* (2000)
Macropodidae	*Dendrolagus matschiei*	6960	36.3	1426.8	McNab (1988a)
Macropodidae	*Lagorchestes conspicillatus*	2660	36	851.2	Withers *et al.* (2000)
Macropodidae	*Macropus eugenii*	4878	36.5	1390.2	Withers *et al.* (2000)
Macropodidae	*Macropus robustus*	29300	36.1	5684.2	Withers *et al.* (2000)
Macropodidae	*Macropus rufus*	32490	35.9	5848.2	Withers *et al.* (2000)
Macropodidae	*Setonyx brachyurus*	2674	36.3	834.3	Withers *et al.* (2000)
Petauridae	*Petaurus breviceps*	127	35.9	89.9	Withers *et al.* (2000)

		M (g)	***T_b*** (°C)	**BMR** (mL O_2 h^{-1})	**Reference**
Petauridae	*Gymnobelideus leadbeateri*	166		102.9	Smith *et al.* (1982)
Phalangeridae	*Spilocuscus maculatus*	4250	34.7	1143.3	Withers *et al.* (2000)
Phalangeridae	*Trichosurus vulpecula*	2005	36	731.6	Withers *et al.* (2000)
Phascolarctidae	*Phascolarctos cinereus*	4765	35.8	1034.0	Withers *et al.* (2000)
Potoroidae	*Bettongia gaimardi*	1385	35.6	641.3	Dawson and Dawson (1981); Withers *et al.* (2000)
Potoroidae	*Bettongia penicillata*	1018	37.2	561.4	Wells (1978); Withers *et al.* (2000)
Potoroidae	*Potorous tridactylus*	976	35.9	416.4	Withers *et al.* (2000)
Potoroidae	*Aepyprimnus rufescens*	2820	36.5	1071.6	Rübsamen *et al.* (1983)
Pseudocheiridae	*Petauroides volans*	1141	35.4	573.9	Withers *et al.* (2000)
Pseudocheiridae	*Pseudocheirus occidentalis*	861	36.5	409.0	Withers *et al.* (2000)
Pseudocheiridae	*Pseudocheirus peregrinus*	916	37.4	430.5	Kinnear and Shield (1975)
Tarsipedidae	*Tarsipes rostratus*	10	36.6	29.0	Withers *et al.* (2000)
Vombatidae	*Lasiorhinus latifrons*	29917	35.3	2991.7	Withers *et al.* (2000)
Notoryctemorphia					
Notoryctidae	*Notoryctes caurinus*	34	30.8	21.4	Withers *et al.* (2000)
Peramelemorphia (9)		**860.3**	**35.0**	**366.82**	
Peroryctidae	*Echymipera kalabu*	695	35	341	Withers *et al.* (2000)
Peroryctidae	*Echymipera rufescens australis*	616	34.6	302	Withers *et al.* (2000)
Peroryctidae	*Echymipera rufescens rufescens*	1276	35.2	541	Withers *et al.* (2000)
Peramelidae	*Isoodon auratus*	428	33.8	150	Withers *et al.* (2000)
Peramelidae	*Isoodon macrourus*	1551	35.9	574	Withers *et al.* (2000)
Peramelidae	*Isoodon obesulus*	717	33.9	222	Withers *et al.* (2000)
Peramelidae	*Macrotis lagotis*	1294	35	450	Withers *et al.* (2000)
Peramelidae	*Perameles gunni*	837	35.2	420	Withers *et al.* (2000)
Peramelidae	*Perameles nasuta*	645	36.1	316	Withers *et al.* (2000)
Monotremata (4)		**1982.6**	**32.3**	**386.1**	
Ornithorhynchidae	*Ornithorhynchus anatinus*	693	34	194	McNab (1970)
Tachyglossidae	*Zaglossus bruijni*	10300	30.8	1215	McNab (1984)
Tachyglossidae	*Tachyglossus aculeatus*	2725	30.7	431	McNab (1984)
Tachyglossidae	*Tachyglossus setosus*	3580	30	548	McNab (1984)

Appendix B. Determination of Q_{10} from an exponential relationship relating metabolic rate and body temperature

Q_{10} can be calculated as the ratio of two rates R measured at temperatures T_a and T_b, provided that T_a and T_b are separated by 10 °C:

$$Q_{10} = \frac{R_{T_a}}{R_{T_b}} \tag{1}$$

$$T_a - T_b = 10 \tag{2}$$

Alternatively, measurements can be obtained at a range of temperatures and an exponential equation of the form $R = \mathrm{a}\, e^{\mathrm{b}\, T}$ can be fitted to the data to describe the relationship between R and T, thus

$$R_{T_a} = \mathrm{a} \cdot e^{\mathrm{b} \cdot T_a} \tag{3}$$

$$R_{T_b} = \mathrm{a} \cdot e^{\mathrm{b} \cdot T_b} \tag{4}$$

Assuming again that T_a and T_b differ by 10 °C, equations (2), (3), and (4) can be substituted into equation (1) and solved to eliminate R and T such that

$$\begin{aligned} Q_{10} &= \frac{\mathrm{a} \cdot e^{\mathrm{b} \cdot T_a}}{\mathrm{a} \cdot e^{\mathrm{b} \cdot T_b}} \\ &= e^{(\mathrm{b} \cdot T_a - \mathrm{b} \cdot T_b)} \\ &= e^{\mathrm{b}(T_a - T_b)} \\ &= e^{10\mathrm{b}} \end{aligned} \tag{5}$$

Q_{10} can therefore be calculated only from b, which can either be taken from the relationship $R = \mathrm{a}\, e^{\mathrm{b}\, T}$ or from the slope of linear regression relating $\ln(R)$ and T,

$$\ln(R) = \mathrm{b}\, T + \ln(\mathrm{a})$$

Determination of b in this manner is advantageous because it also allows for calculation of SE and 95% confidence intervals for b, and therefore also for Q_{10}.

Appendix C. A model for calculation of the cost of burrow construction for semi-fossorial mammals

When measured for short lengths of tunnel, burrowing net cost of transport (NCOT$_b$) accounts only for the cost of removing soil from the undisturbed face and moving along a relatively short length of horizontal tunnel. This measurement therefore neglects the additional costs of pulling soil along a longer tunnel, raising soil to the surface, and moving the animals own body mass between the workface and the surface. The following model is based largely on the burrow systems of *Notomys alexis* (Lee *et al.* 1984), but is generally applicable to semi-fossorial species and can be used to estimate the total cost of burrow construction for any system that is constructed in three stages: (1) excavation of a sloping section of known declination to a given depth. (2) Construction of a blind-ending horizontal tunnel from the end of the sloping tunnel. (3) Construction of a vertical shaft excavated upward from the junction of the horizontal and sloping tunnels - spoil generated by this excavation is used to backfill the sloping tunnel. The total cost of construction (E_{TOT}, J) is equal to the sum of the costs of constructing the individual components. Thus $E_{TOT} = E_{sloping} + E_{horizontal} + E_{vertical}$.

Sloping Tunnel

The model assumes that the energy cost of burrow constructing the sloping component of the system ($E_{sloping}$, J) can be calculated using the equation:

$$E_{sloping} = E_e + E_{sh} + E_{sv} + E_{ah} + E_{av} \qquad (1)$$

Where E_e = cost of removing soil from the undisturbed face (cost of excavation)
E_{sh} = cost of moving soil horizontally to the burrow entrance
E_{sv} = cost of moving soil vertically to the burrow entrance
E_{ah} = cost of moving the animal horizontally to the burrow entrance
E_{av} = cost of moving the animal vertically to the burrow entrance

If no significant effect of total excavation length on net cost of transport by burrowing (NCOT$_b$, J m^{-1}) can be detected, it can be assumed that NCOT$_b$ multiplied by the distance burrowed provides a reasonable estimate of E_e (J). Therefore, given that d is burrow depth (m), and θ is the angle at which the burrow descends, relative to horizontal

$$E_e = \mathrm{NCOT}_b \, {}^{d}/_{\sin\theta} \tag{1}$$

The energy cost of moving soil horizontally to the burrow surface (E_{sh}, J) can be calculated as the product of the mass of soil moved (M_s, g) the mean horizontal distance through which it must be moved (½ l_h, m) and the energy cost of pushing one gram of soil one meter (k, J g^{-1} m^{-1}, after (Vleck 1979)). M_s is equal to $A_b \, \rho \, {}^{d}/_{\sin\theta}$ where A_b = burrow cross-sectional area (m^2), ρ = soil bulk density (g m^{-3}); l_h is equal to ${}^{d}/_{\tan\theta}$.

$$E_{sh} = \tfrac{1}{2} \, k \, M_s \, {}^{d}/_{\tan\theta} \tag{2}$$

Evaluation of *k* requires knowledge of the shear strength and cohesion between the loose spoil pushed by the scorpion and the undisturbed compact soil over which it is dragged. Alternatively, it may be assumed that the scorpion effectively carries spoil to the surface (i.e. the cost of overcoming friction whilst dragging the soil is similar to the energy required to carry the soil). In this case it may be further assumed that the cost of moving 1 g of load 1 m is equal to the cost of moving 1 g of body mass 1 m, as has been shown for mammals (Taylor *et al.* 1980), a hermit crab (Herreid and Full 1986) and several species of ant (Lighton *et al.* 1987; Bartholomew *et al.* 1988; Duncan and Lighton 1994). It should be noted, however, that in certain cases the cost of moving 1 g of load is substantially less than moving 1 g of body mass. Women of certain African tribes, for example, can carry loads equal to 20% of their body mass without incurring an additional energetic cost (Maloiy *et al.* 1986) and rhinoceros beetles (*Xylorctes thestalus*) can move 1 g of load five times more cheaply than they can move 1 g of their own body mass (Kram 1996). Although it is not clear how rhinoceros beetles are able to cheaply move loads, the African women appear to be able to do so by conserving mechanical energy through a pendulum-like transfer of energy between gravitational potential energy and kinetic energy of the centre of mass (Heglund *et al.* 1995). Assuming that the costs of moving equivalent load and body masses are equal, *k* can be evaluated by multiplying the net cost of pedestrian transport ($NCOT_p$, J m^{-1}) by the ratio of total soil mass to animal mass (${}^{M_s}/_{M_a}$). E_{sh} can therefore be estimated using the equation:

$$E_{sh} = \tfrac{1}{2} \, {}^{d}/_{\tan\theta} \left({}^{M_s}/_{M_a}\right) NCOT_p \tag{3}$$

The energy cost of working against gravity to raise the soil excavated during construction of an angled burrow to the surface (E_{sv}, J) can be calculated as the product of the mass of soil removed (M_s, g), the mean depth through which it must be moved (½ d, m), and the amount of mechanical work necessary to move a load against gravity (g, 9.8×10^{-3} J g^{-1} m^{-1}) divided by the efficiency with which metabolic work is done against gravity (α)

$$E_{sv} = \tfrac{1}{2}\, d\, M_s\, {}^{g}/_{\alpha} \qquad \text{(4) (After Vleck (1981), eqn 2)}$$

The energy cost of the horizontal component of motion along the length of the tunnel (E_{ah}, J) depends upon the total horizontal distance travelled and the net cost of pedestrian transport ($NCOT_p$, J m^{-1}). In turn, the total horizontal distance travelled depends on the number of trips the animal makes to the surface to deposit spoil (n_t), which is determined by the maximum load size that the animal can move. The burrow is therefore excavated in portions equal in size to ${}^{l}/_{n_t}$, of which the horizontal component is equal to ${}^{l}/_{n_t}$ or ${}^{d}/_{(n_t \tan\theta)}$. Following excavation of a segment, the animal must travel to the surface and return to the excavation face, such that each newly excavated segment is traversed twice following excavation and twice more following excavation of each new segment. The total distance travelled is therefore equal to $2\Sigma(1, 2, \ldots, n_t\text{-}1, n_t)d/(n_t \tan\theta)$ and the cost of the horizontal component of motion along the burrow can be determined with the equation:

$$E_{ah} = NCOT_p\, 2\Sigma(1, 2, \ldots, n_t\text{-}1, n_t)\, {}^{d}/_{n_t \tan\theta} \qquad (5)$$

Calculation of the cost of vertical movement (E_{av}, J) along the length of the burrow follows a similar pattern. In this case, $NCOT_P$ is replaced with the energetic cost of raising the animal's mass vertically minus the gravitational potential energy that can be harnessed and used to reduce the cost of moving down an incline. If we let β equal the efficiency with which gravitational potential energy is harnessed to reduce the energetic cost of descent, then

$$\begin{aligned} E_{av} &= [M_a\, ({}^{g}/_{\alpha})\, \Sigma(1, 2, \ldots, n_t\text{-}1, n_t)\, {}^{d}/_{n_t}] - [M_a\, (g\,\beta)\, \Sigma(1, 2, \ldots, n_t\text{-}1, n_t)\, {}^{d}/_{n_t}] \\ &= M_a\, g\, ({}^{1}/_{\alpha} - \beta)\, \Sigma(1, 2, \ldots, n_t\text{-}1, n_t)\, {}^{d}/_{n_t} \qquad (6) \end{aligned}$$

Horizontal Tunnel

Calculation of the cost of construction of a horizontal tunnel of length l at the end of the sloping tunnel follows a similar logic to that described above. Again,

$$E_{horizontal} = E_e + E_{sh} + E_{sv} + E_{ah} + E_{av}$$

Following equation (1) above, E_e is equal to the distance that must be excavated (l, m) multiplied by NCOT_b,

$$E_e = l\,\mathrm{NCOT}_b \tag{7}$$

Again, E_{sh} is equal to the mean distance through which the soil much be moved multiplied by M_s and the ratio of soil to animal mass. In this case however, the soil must also be moved through the sloping tunnel to be deposited on the surface, thus

$$E_{sh} = (\tfrac{1}{2}\,{}^{d}/_{\tan\theta} + l)\,({}^{M_s}/_{M_a})\,NCOT_p \tag{8}$$

Because this section of tunnel is horizontal, mean depth is equal to d, so E_{sv} can be calculated from modification of equation (4)

$$E_{sv} = d\,M_s\,{}^{g}/_{\alpha} \tag{9}$$

The animal must now travel to the surface and return to the excavation face through the sloping section of tunnel and must traverse it twice following excavation of each new segment, in addition to traversing each newly excavated segment twice following excavation and twice more following excavation of each new segment.

$$\begin{aligned} E_{ah} &= NCOT_p\,2\Sigma(1, 2, \ldots, n_t\text{-}1, n_t)\,{}^{d}/_{n_t \tan\theta} + 2\,n_t\,({}^{d}/_{\tan\theta})\,\mathrm{NCOT}_p \\ &= 2\,\mathrm{NCOT}_p\,(\Sigma(1, 2, \ldots, n_t\text{-}1, n_t)\,{}^{d}/_{n_t \tan\theta} + n_t\,{}^{d}/_{\tan\theta}) \end{aligned} \tag{10}$$

Because this section of burrow is horizontal, the only vertical component to movement is travel to the surface to deposit spoil: excavation has no vertical component, therefore

$$E_{av} = M_a\, g\, ({}^{1}/_{\alpha} - \beta)\, n_t\, d \qquad (11)$$

Vertical Tunnel

Construction of the vertical tunnel follows a slightly different pattern because spoil is not deposited on the surface, but is used to backfill the sloping tunnel. Again,

$$E_{vertical} = E_e + E_{sh} + E_{sv} + E_{ah} + E_{av}$$

Excavation costs are determined in an analogous manner as for the sloping and horizontal sections, and assume that the cost of excavating in an upward direction is similar to the cost of excavating horizontally or down:

$$E_e = d\, \mathrm{NCOT}_b \qquad (12)$$

Because the excavated soil falls from the excavation face and then must be transported to the plug, it must be moved to a mean horizontal distance of ½ $d\,cos\theta$ from the entrance and must therefore be moved a mean horizontal distance of $({}^{d}/_{tan\theta} - ½\, d\, sin\theta)$, thus

$$E_{sh} = ({}^{d}/_{tan\theta} - ½\, d\, sin\theta)\, ({}^{M_s}/_{M_a})\, NCOT_p \qquad (13)$$

Because the excavated soil falls from the excavation face and then must be transported to the plug, it must be moved from the burrow floor to a mean vertical distance of ½ $d\,sin\theta$ from the surface, and must therefore be moved a mean distance of (d - ½ $d\,sin\theta$) against gravity, thus

$$E_{sv} = (\mathrm{d} - ½\, d\, sin\theta)\, M_s\, {}^{g}/_{\alpha} \qquad (14)$$

Assuming again that this portion of the burrow is excavated in segments appropriately sized for the animal to carry, the burrow is excavated is segments of which the horizontal component is equal to $({}^{d}/_{tan\theta} - ½\, d\, sin\theta)/n_t$ and by substitution into equation (5)

$$E_{ah} = NCOT_p\, 2\Sigma(1, 2, \ldots, n_t\text{-}1, n_t)\, ({}^{d}/_{tan\theta} - ½\, d\, sin\theta)/_{n_t} \qquad (15)$$

Similarly, excavation occurs in segments with a vertical component of d/n_t, but spoil must also be deposited in segments with a vertical component of $(d - \frac{1}{2} d \sin\theta)/n_t$, so by substitution into equation (6), and assuming that backfilled segments are the same size as excavated ones,

$$E_{av} = M_a\, g\, (1/\alpha - \beta)\, \Sigma(1, 2, \ldots, n_t\text{-}1, n_t)\, [d + (d - \tfrac{1}{2} d \sin\theta)]/n_t \qquad (16)$$

Evaluation of Assumptions

To calculate the total cost of burrow construction, knowledge of a number of burrow parameters and energetic constants is required. The number of trips required to construct a burrow requires knowledge of the amount of soil transported by the animal on each trip to the surface. Figure C.1 shows the effect of mass of spoil (expressed as % of body mass) carried in each trip to the surface on total burrow construction cost for *Notomys alexis* (Chapter 3). Burrow construction costs rise dramatically below about 25% of body mass, but decrease little above 25%. As such, 25% was selected as the appropriate spoil mass for model calculations (Chapter 3).

The efficiency with which metabolic energy can be transferred to useful mechanical work against gravity (α) has been estimated to be in the range of 4.4 – 63% (Cavagna *et al.* 1963; Taylor *et al.* 1972; Full and Tullis 1990b). Within this range, α has little effect on the total cost of burrow construction (Figure C.1). Nevertheless, a conservative position was adopted for model calculations and an efficiency of 4.4% was used (Chapter 3). Although the efficiency with which gravitational potential energy can be harnessed to reduce the cost of moving downhill has been estimated to be as high as 92% (Taylor *et al.* 1972), reducing this value has a minor effect on total burrow construction costs (total cost estimated with efficiencies of 0% and 92% differ by less than 1%). Gravitational potential energy harnessing efficiency was therefore conservatively estimated at 0% for model calculations (Chapter 3).

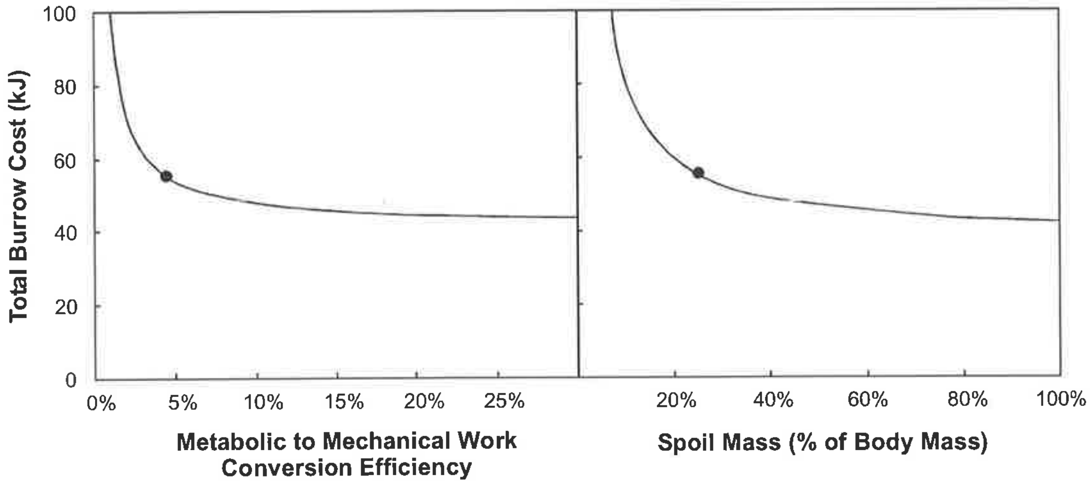

Figure C.1. Effect of efficiency of conversion of metabolic energy to mechanical work against gravity and mass of spoil (expressed as % of body mass) carried in each trip to the surface on total burrow construction cost for *Notomys alexis*. Filled symbol represents spoil mass used in model calculations described in Chapter 3 (4.4% and 25% for conversion efficiency and spoil mass, respectively: Total burrow cost 55.5 kJ).

Glossary of Terms and Symbols

A	Cross-sectional area	m^2
d	depth	m
E	Energy	J
g	Cost of moving 1 g a distance of 1 m against gravity	9.8×10^{-3} J g^{-1} m^{-1}
k	Mass- and distance-specific cost	J g^{-1} m^{-1}
l	Length	m
M	Mass	g
$NCOT_b$	Net cost of transport by burrowing	J m^{-1}
$NCOT_p$	Net cost of pedestrian transport	J m^{-1}
n	number	
α	Efficiency of conversion of metabolic energy to work against gravity	
β	Efficiency of harnessing gravitational potential energy	
θ	Angle of burrow declination	
ρ	Soil density	g m^{-3}

Subscripts

a	Animal
b	Burrow
e	Excavation
h	In horizontal plane
s	Soil
t	Trips to surface
TOT	Total
v	In vertical plane

Appendix D. Body masses, basal metabolic rates (BMR), habitat (arid/mesic) and foraging mode (fossorial/semi-fossorial) of burrowing mammals

Species	Mass (g)	BMR (mL O_2 min^{-1})			Reference
Monotremata					
Ornithorhynchidae					
Ornithorhynchus anatinus (Or)	1311	7.93	mesic	semi	Dawson *et al.* (1979)
Metatheria					
Dasyuridae					
Antechinus swainsoni (Aw)	66.9	1.05	mesic	semi	Chappell and Dawson (1994)
Dasyuroides bymie (Db)	115	1.25	arid	semi	Dawson and Dawson (1981)
Sminthopsis crassicaudata (SC)	14.2	0.26	arid	semi	Chappell and Dawson (1994)
Notoryctidae					
Notoryctes caurinus (Nc)	34	0.36	arid	fossorial	Withers *et al.* (2000)
Thylacomydae					
Macrotis lagotis (Ml)	1011	5.97	arid	semi	Hulbert and Dawson (1974)
Vombatidae					
Lasiorhinus latifrons (Ll)	18250	27.38	arid	semi	Wells (1978)
Eutheria					
Carnivora					
Canidae					
Fennecus zerda (Fz)	1215	9.72	arid	semi	Maloiy *et al.* (1982)
Mustelidae					
Mustela vision (Mv)	703.7	8.58	mesic	semi	Farrell and Wood (1968)
Taxidea taxus (TT)	9000	45.00	mesic	semi	Harlow (1981)
Edentata					
Dasypodidae					
Cabassous centralis (CC)	3810	13.34	mesic	semi	McNab (1980)
Chaetophractus nationi (Cn)	2150	9.32	arid	semi	McNab (1980)
Chaetophractus vellerosus (Cv)	1110	5.18	arid	semi	McNab (1980)
Chaetophractus villosus (Cs)	4540	13.47	arid	semi	McNab (1980)
Dasypus novemcincus (Dn)	3510	19.66	mesic	semi	McNab (1980); Boggs *et al.* (1998)
Euphractus sexcinctus (Es)	8190	20.61	mesic	semi	McNab (1980)
Priodontes maximus (Pm)	45190	50.46	mesic	semi	McNab (1980)
Zaedyus pichiy (Zp)	1740	6.67	mesic	semi	McNab (1980)
Insectivora					
Chrysochloridae					
Amblysomus hottentotus (Ah)	69.8	1.59	mesic	fossorial	Kuyper (1979) cited in Bennett and Spinks (1995)
Chrysochloris asiatica (CA)	44	0.86	mesic	fossorial	Bennett *et al.* (1994)
Eremitalpa namibensis (En)	20	0.17	arid	fossorial	Seymour *et al.* (1998)
Erinaceidae					
Erinaceus albiventris (Ea)	450	2.48	mesic	semi	McNab 1980)
Erinaceus concolor (Ec)	822.7	5.79	mesic	semi	Król 1994)
Erinaceus europaeus (Ee)	750	5.63	mesic	semi	Shkolnik and Schmidt-Nielsen (1976)
Hemiechinus auritus (He)	400	2.53	arid	semi	Shkolnik and Schmidt-Nielsen (1976)
Paraechinus aethiopicus (Pa)	450	1.88	arid	semi	Shkolnik and Schmidt-Nielsen (1976)
Talpidae					
Neurotrichus gibbsii (Ng)	10	1.05	mesic	fossorial	Vleck and Kenagy (1987) cited in Lovegrove (1989)
Scalopus aquaticus (Sa)	48	1.13	mesic	fossorial	McNab (1979b)

Species	Mass (g)	BMR (mL O_2 min^{-1})			Reference
Scapanus orarius (So)	59	1.75	mesic	fossorial	Vleck and Kenagy (1987) cited in Lovegrove 1989)
Scapanus townsendi (St)	148	2.89	mesic	fossorial	Vleck and Kenagy (1987) cited in Lovegrove 1989)
Tenrecidae					
Setifer setosus (SS)	530	2.03	mesic	semi	McNab (1980)
Lagomorpha					
Ochotonidae					
Ochotona daurica (Od)	127.7	3.96	arid	semi	Weiner and Górecki (1981)
Pholidota					
Manidae					
Manis pentadactyla (Mp)	3638	11.13	mesic	semi	Heath and Hammel (1986)
Rodentia					
Aplodontidae					
Aplodontia rufa (Ap)	630	4.62	mesic	semi	McNab (1979b)
Bathyergidae					
Bathyergus janetta (Bj)	406	3.59	arid	fossorial	Lovegrove (1986b)
Bathyergus suillus (Bs)	620	5.06	mesic	fossorial	Lovegrove (1986b)
Cryptomys bocagei (Cb)	94	1.16	mesic	fossorial	Bennett *et al.* (1994)
Cryptomys damarensis (Cd)	138	1.31	arid	fossorial	Lovegrove (1986a); Lovegrove and Knight-Eloff (1988)
Cryptomys hottentotus amatus (Ct)	79.5	0.92	mesic	fossorial	Bennett *et al.* (1994); Marhold and Nagel (1995)
Cryptomys hottentotus darlingi (Cl)	60	0.98	mesic	fossorial	Bennett *et al.* (1993)
Cryptomys h. hottentotus (CE)	75	1.13	arid	fossorial	Bennett *et al.* (1992)
Cryptomys mechowi (Cm)	267	2.67	mesic	fossorial	Bennett *et al.* (1994)
Georhychus capensis (Gc)	197	1.94	mesic	fossorial	Du Toit *et al.* (1985)
Heliophobius argentocinereus (Ha)	88	1.25	arid	fossorial	McNab (1979b)
Heterocephalus glaber (Hg)	32	0.34	arid	fossorial	McNab (1966b); Withers and Jarvis (1980)
Ctenomyidae					
Ctenomys fulvus (Cf)	300	3.15	arid	semi	Contreras (1983) cited in McNab (1988a)
Ctenomys maulinus (Ca)	215	3.12	mesic	semi	Contreras (1983) cited in McNab (1988a)
Ctenomys peruanus (Cp)	490	3.68	mesic	semi	McNab (1979b)
Ctenomys sp. (Cy)	197	2.17	mesic	semi	Contreras (1983) cited in McNab (1988a)
Echimyidae					
Proechimys iheringi (PH)	223.9	3.07	mesic	semi	Barros *et al.* (1998)
Proechimys yonenagae (Py)	243.3	2.55	mesic	semi	Barros *et al.* (1998)
Geomyidae					
Geomys bursaris (GB)	197	2.30	mesic	fossorial	Bradley and Yousef (1975)
Geomys pinetis (Gp)	173	2.22	mesic	fossorial	McNab (1966b); Ross (1980)
Thomomys bottae (Tb)	143	2.00	mesic	fossorial	Vleck (1979)
Thomomys talpoides (Tt)	106.8	2.37	mesic	fossorial	Gettinger (1975)
Thomomys umbrinus (TU)	85	1.20	arid	fossorial	Bradley *et al.* (1974)
Heteromyidae					
Dipodomys deserti (Dd)	106	1.54	arid	semi	McNab (1979a)
Dipodomys merriami (Dm)	34.7	0.69	arid	semi	Dawson (1955)
Dipodomys microps (Di)	57.2	1.12	arid	semi	Breyen *et al.* (1973)
Dipodomys panamintinus (DP)	56.9	1.14	arid	semi	Dawson (1955)
Heteromys anomalus (Ht)	69.3	1.67	mesic	semi	McNab (1979a)

Species	Mass (g)	BMR (mL O_2 min^{-1})			Reference
Liomys irroratus (Li)	48.1	0.90	arid	semi	Hudson and Rummel (1966b)
Liomys salvani (Ls)	43.8	0.78	arid	semi	Hudson and Rummel (1966b)
Microdipodops pallidus (Ho)	15.2	0.33	arid	semi	Bartholomew and MacMillen (1960)
Perognathus californicus (Pf)	22	0.36	arid	semi	Tucker (1965)
Perognathus hispidus (Pu)	39.5	0.82	arid	semi	Wang and Hudson (1970)
Perognathus intermedius (Pi)	15	0.30	arid	semi	Bradley *et al.* (1975)
Perognathus longimembris (Pl)	8.9	0.16	arid	semi	Chew *et al.* (1967)
Muridae					
Arvicolinae					
Microtus agrestis (Ma)	28	1.06	mesic	semi	McDevitt and Speakman (1996)
Microtus montanus (Mo)	30.8	1.36	arid	semi	Packard (1968)
Microtus pinetorum (Pp)	25.5	0.97	mesic	semi	McNab (1979b)
Cricetinae					
Mesocricetus auratus (MA)	120	1.72	arid	semi	Tegowska and Gebczynski (1975)
Gerbillinae					
Desmodillus auricularis (Da)	71.9	1.46	arid	semi	Downs and Perrin (1994)
Gerbillus allenybi (Ga)	35.3	0.65	arid	semi	Haim (1984)
Gerbillus manus (Gm)	28.4	0.37	arid	semi	Haim (1984)
Meriones unguicalatus (Mu)	66.9	1.27	arid	semi	Weiner and Górecki (1981)
Tatera leucogaster (Tl)	157.6	2.21	mesic	semi	Downs and Perrin (1994)
Murinae					
Apodemus mystacinus (Am)	40.4	0.93	mesic	semi	Haim (1987)
Apodemus sylvaticus (Ay)	23.9	0.72	mesic	semi	Haim (1987)
Hydromys chrysogaster (Hc)	790	7.73	mesic	semi	Dawson and Fanning (1981)
Leggadina hermannsburgensis (Lh)	12.2	0.39	arid	semi	MacMillen and Lee (1970)
Notomys alexis (Na)	32.3	0.75	arid	semi	MacMillen and Lee (1970)
Notomys cervinus (Ne)	34.2	0.70	arid	semi	MacMillen and Lee (1970)
Praomys natalensis (Pn)	41.5	0.55	arid	semi	Haim and Fourie (1980)
Pseudomys gracilicaudatus (Pg)	79.8	1.40	mesic	semi	Dawson and Dawson (1981)
Rhizominae					
Cannomys badius (Ci)	344	2.87	mesic	semi	McNab (1979b)
Tachyoryctes splendens (Ts)	191	2.51	mesic	fossorial	McNab (1979b)
Sigmodontinae					
Baiomys taylori (Bt)	7.3	0.24	arid	semi	Hudson (1965)
Peromyscus eremicus (Pe)	17.4	0.45	arid	semi	MacMillen (1965)
Octodontidae					
Aconaemys fuscus (Af)	112	2.02	mesic	semi	Contreras (1983) cited in McNab (1988a)
Octodon degus (Oc)	179.9	2.48	mesic	semi	Bozinovic and Novoa (1997)
Spalacopus cyanus (Su)	134.7	1.86	mesic	semi	McNab (1979b); Contreras (1986)
Pedetidae					
Pedetes capensis (Pc)	2300	12.27	arid	semi	Müller *et al.* (1979)
Sciuridae					
Ammospermophilus leucurus (Al)	96	1.65	arid	semi	Hudson (1962)
Cynomys ludovicianus (Cu)	1112	7.04	arid	semi	Reinking *et al.* (1977)
Marmota monax (Mm)	2650	11.04	mesic	semi	Benedict (1938)
Spermophilus armatus (Sr)	320	2.45	mesic	semi	Hudson *et al.* (1972)
Spermophilus beecheyi (Sy)	600	5.40	arid	semi	Baudinette (1972)
Spermophilus beldingi (Sb)	303	2.12	mesic	semi	Hudson *et al.* (1972)
Spermophilus lateralis (Se)	274	2.06	mesic	semi	Hudson *et al.* (1972)

Species	Mass (g)	BMR (mL O_2 min^{-1})			Reference
Spermophilus mohavensis (Sm)	240	1.88	arid	semi	Hudson *et al.* (1972)
Spermophilus richardsoni (SR)	274	2.19	arid	semi	Hudson *et al.* (1972)
Spermophilus spilosoma (Ss)	174	1.54	arid	semi	Hudson *et al.* (1972)
Spermophilus tereticaudus (Sc)	167	1.56	arid	semi	Hudson *et al.* (1972)
Spermophilus townsendii (Sw)	229	1.76	arid	semi	Hudson *et al.* (1972)
Spermophilus tridecemlineatus (SM)	182	1.73	mesic	semi	Hudson *et al.* (1972)
Xerus inauris (Xi)	542	5.44	mesic	semi	Haim *et al.* (1987)
Spalacidae					
Spalax ehrenbergi 2n = 52* (S2)	116	1.84	mesic	fossorial	Nevo and Shkolnik (1974)
Spalax ehrenbergi 2n = 58* (S8)	120.5	1.73	arid	fossorial	Nevo and Shkolnik (1974)
Spalax ehrenbergi 2n = 60* (S0)	121	1.25	arid	fossorial	Nevo and Shkolnik (1974)
Spalax leucodon (Sl)	201	2.48	mesic	fossorial	McNab 1979b)
Tublidentata					
Orycteropodidae					
Orycteropus afer (Oa)	48000	102.40	mesic	semi	McNab (1984)

* These are three of the four chromosomal forms of the *Spalax ehrenbergi* superspecies. Each constitutes a good, though as yet unnamed, biological species (Nevo 1991).

Appendix E. Description of phylogenetic derivations for burrowing mammals

Classification at sub-ordinal levels follows that of Nowak (1999).

Monotremata diverged from other therian lineages during Early Jurassic (Luo *et al.* 2001). The Metatheria/Eutheria split was dated according to Kumar and Hedges (1998). Divergences within Marsupialia were dated according to Kirsch *et al.* (1997)

Rodentia: Hystricognathi divergence and divergence within Hystricognath and Non-Hystricognath rodents dated according to Sarich (1985). The Geomyidae/Heteromyidae divergence was dated according to Fahlbusch (1985). Divergences within Heteromyidae were dated according to Hafner and Hafner (1983), with data modified in accordance with a *Mus/Rattus* split of 20 MYA. Within Octodontidae, the Ctenomyinae/Octodontinae split was dated according to Lessa and Cook (1998). Within Muridae, divergences at subfamily level (possibly represents a hard polytomy) were dated according to Robinson *et al.* (1997). Other rodent divergences were dated as follows: Spalacinae divergence from other Murids: Catzeflis *et al.* (1992). Spalacinae/ Rhizominae divergence: Robinson *et al.* (1997). Divergence within Arvicolinae (*Microtus* and *Pitymys*): Chaline and Graf (1988). Divergence within Murinae: Watts and Baverstock (1995). Divergence within Spalacinae; *Spalax leucodon/S. ehrenbergi*: Robinson *et al.* (1997), Divergence within *Spalax ehrenbergi* superspecies: Nevo *et al.* (1999), Geomyidae: Smith (1998), Bathergidae: Allard and Honeycutt (1992); Faulkes *et al.* (1997), Sciuridae: Using a divergence time at the sub-genus level of 5 MYA (Smith and Coss 1984), species level divergence was assumed to have occurred 2.5 MYA and genus-level divergence was assumed to have occurred 10 MYA. A similar timescale was adopted for other rodent species for which divergence times are unavailable. Pedetidae: *Pedetes capensis* was placed at the most ancient polytomy of the Non-Hystricognath rodents, which places it a similar divergence time to the proposed by Matthee and Robinson (1997). Echimyidae: Divergence within *Proechimys*: Corti and Aguilera (1995)

Carnivora: The Canidae/Mustelidae split was dated according to Ledje and Arnason (1996). Divergence within Mustelidae (at the genus level) was taken to have occurred 20 MYA based on a *Mustela/Lutra* Divergence of 20-25 MYA and species level divergence within *Mustela* of 15 MYA (Wayne *et al.* 1989)

Insectivora: Divergence of Erinaceidae/Talpidae, Chrysochloridae and Tenrecidae was assumed to have occurred as a trifurcation dated using the Tenrecidae/Erinaceidae Split (75 MYA: Madsen *et al.* 2001). Divergences within Talpidae were dated according to Yates and Greenbaum (1982). Given that appropriate divergence times for Erinaceidae and Chrysochloridae were unavailable, it was assumed that diversification within these groups at the following levels was evenly spaced through time: Superfamily, Family, Subfamily, Genus, Subgenus, and Species. For Erinaceidae, this produced a soft polytomy around 27 MYA where *Erinaceus*, *Hemiechinus* and *Paraechinus* diverged and another around 7.5 MYA where the three species of *Erinaceus* diverged. For Chrysochloridae, this produced a soft polytomy around 38 MYA where *Eremitalpa*, *Chrysochloris* and *Amblysomus* diverged.

Xenarthra: Given that appropriate divergence times were unavailable, it was assumed that diversification at the following levels was evenly spaced through time: Order, Superfamily, Family, Subfamily, Genus, Subgenus, and Species. This produced a soft polytomy around 40 MYA where the six armadillo genera considered in this study diverged and another around 11 MYA where the three species of *Chaetophractus* diverged.

Appendix F. Body masses (M, g), burrow cross-sectional areas (A_b, cm^2), and nest chamber volumes (V_n, cm^3) of fossorial mammals, semi-fossorial mammals, birds, reptiles and other invertebrates and vertebrates

	M	A_b (cm^2)	V_n (L)	Reference
		Colonial Fossorial Mammals		
Cryptomys anselli	86.5	28.3		Scharfe *et al.* (2001)
Cryptomys damarensis	152.1	30.6	4.2	Lovegrove (1989); Roper *et al.* (2001); Scharfe *et al.* (2001)
Cryptomys hottentotus	65.8	25.8	1.8	Genelly (1965); Davies and Jarvis (1986); Spinks *et al.* (1999)
Cryptomys h. natalensis	97.0	15.9	4.5	Hickman (1979) cited by Scharfe *et al.* (2001)
Cryptomys mechowi	298.5	63.6	14.1	Scharfe *et al.* (2001)
Spalacopus cyanus	90	28.3		Begall and Gallardo (2000)
		Solitary Fossorial Mammals		
Bathyergus suillus	945	254.5		Davies and Jarvis (1986)
Condylura cristata	40	12.6	5.3	Hickman (1983)
Geomys attawateri	134	37.4		Williams and Cameron (1990)
Geomys bursaris	202	48.9		Best (1973)
Georychus capensis	189	68.7		Du Toit *et al.* (1985); Roper *et al.* (2001)
Heliophobius argenteocinereus	160	19.6		Jarvis and Sale (1971)
Heterocephalus glaber	36	7.9		Jarvis and Sale (1971); Lovegrove (1989)
Orthogeomys heterodus	600	50.3	47.7	Sisk and Vaughn (1984)
Pappogeomys castanops	316	72.2	28.2	Best (1973); Hickman (1977)
Scapanus orvarius	59	20.7	3.6	Kuhn *et al.* (1966); Vleck and Kenagy (1987) cited in Lovegrove (1989)
Scapanus townsendii	148	32.0		Vleck and Kenagy (1987) cited in Lovegrove (1989)
Spalax ehrenbergi	154	36.3	133	Heth (1989)
Tachyoryctes spledens	324	28.3		Jarvis and Sale (1971)
Thomomys bottae	119	34.0		Vleck (1979; 1981); Vleck and Kenagy (1987) cited in Lovegrove (1989)
Thomomys monticola	77.3		48.8	Ingles (1952)
Thomomys talpoides	107	22.7		Banfield (1974); Vleck and Kenagy (1987) cited in Lovegrove (1989)
		Semi-Fossorial Mammals		
Apodemus sylvaticus	23.9	7.1		Jennings (1975)
Bandicota bengalensis	200	46.4		Pouché *et al.* (1982)
Canis latrans	13500	946.9	119.5	Ryon (1986)
Canis lupus	38500	1179.3	194.1	Ryon (1977)
Cynomys leucurus	1050	78.5		Burns *et al.* (1989)
Cynomys leucurus	1050	153.9	5.8	Cooke and Swiecki (1992)
Cynomys parvidens	1000		8.7	Egoscue and Frank (1984)
Dicrostomys torquatus	73	31.7	1.0	Banfield (1974)
Dipodomys nelsoni	84.7	45.4		Best *et al.* (1988)
Dipodomys ordii	48.8	29.7		Laundré (1989)
Dipodomys spectabilis cratodon	117	45.4		Best *et al.* (1988)
Dipodomys s. zygomaticus	116.5	51.5		Best *et al.* (1988)
Euphractus sexcinctus	8200	314.2		Carter and Encarinacao (1983)
Eutamias minimus	42.9	11.4		Banfield (1974)
Eutamias sibiricus	113	12.9	5.8	Kawamichi (1989)

	M	A_b (cm^2)	V_n (L)	Reference
Hyaena brunnea	42250	3318.3		Owens and Owens (1979)
Lasiorhinus latifrons	26000	754.4		Flösser (1984)
Lasiorhinus krefftii	35000	2322.1		Shimmin, G.A. and White, C.R., Unpublished
Lemmiscus curtatus	21	12.6	1.0	Mullican and Keller (1987)
Lemmus sibiricus	67.8		1.9	Banfield (1974)
Marmota monax	2850	506.7	29.0	Banfield (1974)
Meles meles	9000	490.9	70.6	Roper *et al.* (1991)
Mesocricetus auratus	93.9	15.2	1.8	Gattermann *et al.* (2001)
Microcavia australis	200	78.5		Rood (1970)
Microtus montanus	30.8	28.3		Laundré (1989)
Microtus ochrogaster	51	17.3	1.3	Mankin and Getz (1994)
Ornithorhynchus anatinus	1311	86.6	6.2	Serena (1994)
Oryctolagus cuniculus	1500	217.0		Stott (1996)
Pedetes capensis	3000	240.5		Butynski and Mattingly (1979)
Peroognathus parvus	17.05		0.2	Banfield (1974)
Peromyscus maniculatus	23.1	19.2		Laundré (1989)
Priodontes maximus	45000	1164.2		Carter and Encarinacao (1983)
Rattus villosissimus	190.8	19.6	1.8	Carstairs (1980); Predavec and Dickman (1994)
Saccostomus campestris	46.6	15.0	1.2	Ellison (1993)
Spermophillus columbianus	492	62.1		Banfield (1974)
Spermophillus elegans	290	35.3		Laundré (1989)
Spermophillus lateralis	231	20.3	1.9	Banfield (1974)
Spermophillus richardsonii	405	45.6		Banfield (1974)
Spermophillus townsendii	229	34.2		Laundré (1989)
Synaptomys cooperi	28.3	11.4	1.1	Banfield (1974)
Tamias striatus pipilans	106	26.9	1.3	Thomas (1974)
Vombatus ursinus	35000	916.7	117.9	McIlroy *et al.* (1981)
Birds				
Eudyptula minor	1000	249		White, C.R. Unpublished
Merops apiaster	57.5	70.9	3.4	White *et al.* (1978); Ar and Piontkewitz (1992)
Pterodroma h. hypoleuca	174.5	154	5.6	Pettit *et al.* (1982); Grant and Whittow (1983)
Riparia riparia	13.7	18.1	1.9	Birchard and Kilgore (1980); Wickler and Marsh (1981)
Reptiles				
Gopherus polyphemus	3228	340		Ultsch and Anderson (1986); Ultsch and Anderson (1988)
Iguana iguana	1900	123	56.9	Rand and Dugan (1983)
Pituophis m. melanoleucus	687	53.7	1.3	Burger and Zappalorti (1991)
Scorpions*				
Paruroctonus mesahensis (2nd)	2	1.35		Polis *et al.* (1986)
Paruroctonus mesahensis	0.035	0.169		Polis *et al.* (1986)
Urodacus yaschenkoi (2nd)	0.25	0.710		Shorthouse and Marples (1980)
Urodacus yaschenkoi (3rd)	0.55	1.28		Shorthouse and Marples (1980)
Urodacus yaschenkoi (4th)	1.00	1.65		Shorthouse and Marples (1980)
Urodacus yaschenkoi (5th)	1.83	2.25		Shorthouse and Marples (1980)
Urodacus yaschenkoi	3.03	2.94		Shorthouse and Marples (1980)

	M	A_b (cm^2)	V_n (L)	Reference
Opisthophthalamus capensis	3	1.55		Eastwood (1978)
Vermiforms				
Aporrectodea caliginosa	0.13	0.13		Pitkänen and Nuutinen (1997)
Natatolana borealis	0.78	0.31		Taylor and Moore (1995)
Octochaetus multiporus	4.20	0.79		Springett and Gray (1998)
Other Invertebrates				
Ariadna sp.	0.052	0.28		Costa *et al.* (1995)
Calocaris macandreae	2	2.01		Nash *et al.* (1984)
Geolycosa domifex	2.05	1.54		McQueen (1983)
Goneplax rhomboides	17.5	5.27		Rice and Chapman (1971)
Gryllotalpa australis	0.87	1.50		Kavanagh and Young (1989)
Gryllotalpa vineae	3.3	2.54		Bennet-Clark (1970)
Gryllotalpa gryllotalpa	3	1.46		Bennet-Clark (1970)
Hemilepistus reaumuri	0.26	0.57		Shachak (1980); Coenen-Staß (1981)
Nephrops norvegicus	169	25.6		Rice and Chapman (1971)
Scapteriscus acletus	0.6	1.77		Bennet-Clark (1987)
Other Vertebrates				
Cepola rubescens	165	28.3		Atkinson *et al.* (1977)
Periophthalmodon schlosseri	104	50.3		Ishimatsu *et al.* (1998)
Heleioporus eyrei	17.1	9.01		Bailey and Roberts (1981)
Heleioporus albopunctatus	44.6	9.34		Bailey and Roberts (1981)

*For measurements of the burrows of non-adult scorpions, instar number is shown in parentheses

Appendix G. Source code for LIREG_SD

```
DECLARE SUB Large (in$, out$)
'
'This program performs linear regression analysis on randomly selected subsets
'of a data series of x- and y-values separated by comma.  Users may specify
'the number of samples and x-range that subsets are to contain.  Depending on
'file size, the program may create a small tmp file (all_reg.tmp), in which
'subsets are stored whilst processed
'
'REVISION HISTORY
'1.0  April, 2001:  Main module only.  Used a swap file to store subsets.
'     This made data access quite slow, even for small input files.
'1.1  May, 2001:  Subsets now stored in static arrays, however, this limits
'     input file size to approximately 500 pairs
'1.2  July, 2001:  Added Large module (modification of v1.0 main module).
'     For input files smaller than 501 pairs, subsets are stored in static
'     arrays.  For input files larger than or equal to 501 pairs, subsets are
'     written to a temporary swap file.
'1.21 July, 2001:  Addition of additional randomisation procedures.  This will
'     correct potential problems associated with the psedo-random number
'     generator being called millions of times.  Reduced frequency of screen
'     output, previously it was difficult to see processing screens on
'     fast computers - 1333 MHz AMD Athlon Thunderbird test machine
'
CLS
RESET
PRINT
PRINT
PRINT " LIREG_SD"
PRINT
PRINT " LInear REGression of Sub-sampled Data"
PRINT
PRINT
PRINT
PRINT
PRINT " Written by Craig R. White"
PRINT " Dept. of Environmental Biology"
PRINT " University of Adelaide"
PRINT " Adelaide, SA, 5005"
PRINT
PRINT " v1.21"
PRINT " June 2001"
PRINT
PRINT
PRINT
PRINT
PRINT
PRINT " Press any key to continue"
SLEEP
'
TheBeginning:
CLS
RESET
PRINT
PRINT " What is the name and extension of the file containing the data?"
PRINT " The file must contain pairs of x and y values separated by a comma"
INPUT " "; in$
PRINT
'LET in$ = "c:\input.csv"
'
PRINT " What is the name and extension of the file to which results will be written?"
INPUT " "; out$
'LET out$ = "c:\output.csv"
OPEN out$ FOR OUTPUT AS #2
'
'This reads the number of x and y pairs in the file (n&)
PRINT
PRINT " Examining input file..."
LET n& = 0
OPEN in$ FOR INPUT AS #1
DO WHILE NOT EOF(1)
        INPUT #1, x$, y$
        LET n& = n& + 1
        IF n& = 1 THEN
```

```
                LET minx# = VAL(x$)
                LET maxx# = VAL(x$)
        ELSE
                IF (VAL(x$) < minx#) THEN LET minx# = VAL(x$)
                IF (VAL(x$) > maxx#) THEN LET maxx# = VAL(x$)
        END IF
LOOP
CLOSE #1
PRINT
PRINT " Read complete... Insert subliminal message here"
'
IF n& > 500 THEN
        CALL Large(in$, out$)
        GOTO TheBeginning
END IF
'
OPEN in$ FOR INPUT AS #1
DIM x$(n&), y$(n&), xtemp$(n&), ytemp$(n&)
LET i = 0
DO UNTIL i = n&
        LET i = i + 1
        INPUT #1, x$(i), y$(i)
LOOP
CLOSE #1
'
BackTheTruckUp:
CLS
PRINT
INPUT ; " How many sub-sample iterations do you wish to perform"; numofiterations#
IF numofiterations# < 1 THEN GOTO BackTheTruckUp
PRINT
'DIM nout&(numofiterations#), rangeout#(numofiterations#), slopeout#(numofiterations#),
intout#(numofiterations#), r2out#(numofiterations#)
PRINT
'
PRINT , " "; in$; " contains"; n&; "x and y pairs"
PRINT
'
howmanysamples:
PRINT " What is the minimum number of x/y pairs that you would"
INPUT ; "   like the randomly selected subsets to contain"; minnum&
IF minnum& < 3 THEN
        PRINT
        PRINT
        PRINT " This program can not perform regression analysis on data subsets"
        PRINT " containing fewer than 3 values due to problems encountered during"
        PRINT " calculation of r-squared values"
        PRINT
        PRINT " Please re-enter"
        GOTO howmanysamples
END IF
PRINT
PRINT
PRINT " What is the maximum number of x/y pairs that you would"
PRINT "   like the randomly selected subsets to contain?"
PRINT "      Enter a number above the number of pairs in your"
INPUT ; "      data file to set no upper limit ", maxnum&
IF maxnum& > n& THEN LET maxnum& = n&
PRINT
PRINT
PRINT " Your data file has a total x-range of"; (maxx# - minx#)
PRINT " What is the minimum range between max and min x-values that you would"
INPUT ; "   like the randomly selected subsets to contain"; minrange#
PRINT
PRINT
PRINT " What is the maximum range between max and min x-values that you would"
PRINT "   like the randomly selected subsets to contain?"
INPUT ; "   Enter a number above the range of your data set to set no upper limit"; maxrange#
PRINT
PRINT
INPUT ; " Would you like a running estimate of remaining processing time"; counter$
IF counter$ = "y" THEN LET counter& = 1 ELSE LET counter& = 0
'
Commence:
PRINT
PRINT
PRINT " Do you wish to commence calculations"
```

```
INPUT " (n to quit, so to start over, y to continue)"; start$
IF start$ = "n" THEN END
IF start$ = "so" THEN GOTO TheBeginning
IF start$ = "y" THEN GOTO CarryOn ELSE GOTO Commence
'
CarryOn:
'
'this bit takes a note of when the program started running
LET start$ = TIME$
LET starthh& = VAL(LEFT$(start$, 2))
LET startmm& = VAL(MID$(start$, 4, 2))
LET startss& = VAL(RIGHT$(start$, 2))
LET hhpast& = 0
LET mmpast& = 0
LET sspast& = 0
LET cumulativess& = 0
LET lastss& = startss&
LET totaliterationsperformed& = 0
LET clockerror& = 0
'
'this bit selects the random number list to use.  This is done using the
'system time as a changing base
RANDOMIZE (startss& * starthh& * startmm&)
'
'this bit randomly generates subsets of the entire data set
LET iteration# = 0
LET lastiteration# = 0
DO UNTIL iteration# = numofiterations#
'
iteration:
        IF iteration# = 10000 * (INT(iteration# / 10000)) THEN RANDOMIZE (currentss& *
currenthh& * currentmm&)
        '
        LET totaliterationsperformed& = totaliterationsperformed& + 1
        '
        CONST false = 0, true = NOT false
        LET done = false
        LET sumxy# = 0
        LET sumx# = 0
        LET sumy# = 0
        LET sumx2# = 0
        LET sumdevx# = 0
        LET sumdevy# = 0
        LET numbercurrentpair& = 0
        LET nodatapairs& = 0
        '
        LET rejectlev# = RND
        '
        'This creates a temporary file where each new subset will be stored
        'for use in correlation coefficient calculations
        'OPEN "all_reg.tmp" FOR OUTPUT AS #3
        '
        'This next bit will loop until it reaches the end of file 1 (EOF(1))
        DO UNTIL numbercurrentpair& = n&
                '
                LET numbercurrentpair& = numbercurrentpair& + 1
                '
                LET rand# = RND
                IF rand# >= rejectlev# THEN
                        'this counts the number of pairs in the current subset
                        LET nodatapairs& = nodatapairs& + 1
                        '
                        LET xtemp$(nodatapairs&) = x$(numbercurrentpair&)
                        LET ytemp$(nodatapairs&) = y$(numbercurrentpair&)
                        '
                        'this next bit is part of the regression calculation
                        LET sumxy# = sumxy# + (VAL(x$(numbercurrentpair&)) *
 VAL(y$(numbercurrentpair&)))
                        LET sumx# = sumx# + VAL(x$(numbercurrentpair&))
                        LET sumy# = sumy# + VAL(y$(numbercurrentpair&))
                        LET sumx2# = sumx2# + ((VAL(x$(numbercurrentpair&))) ^ 2)
                        '
                        IF nodatapairs& > maxnum& THEN
                                'CLOSE #3
                                LET current$ = TIME$
                                LET currentss& = VAL(RIGHT$(current$, 2))
                                DO UNTIL (currentss& - lastss&) >= 0
```

```
                                        LET lastss& = lastss& - 60
                                LOOP
                                IF currentss& > lastss& THEN
                                        GOSUB timecounter
                                        GOSUB totaltime
                                END IF
                                GOTO iteration
                        END IF
                        IF (nodatapairs& + (n& - numbercurrentpair&)) < minnum& THEN
                                'CLOSE #3
                                LET current$ = TIME$
                                LET currentss& = VAL(RIGHT$(current$, 2))
                                DO UNTIL (currentss& - lastss&) >= 0
                                        LET lastss& = lastss& - 60
                                LOOP
                                IF currentss& > lastss& THEN
                                        GOSUB timecounter
                                        GOSUB totaltime
                                END IF
                                GOTO iteration
                        END IF
                        '
                        IF nodatapairs& = 1 THEN
                                LET minx# = VAL(x$(numbercurrentpair&))
                                LET maxx# = VAL(x$(numbercurrentpair&))
                        ELSE
                                IF (VAL(x$(numbercurrentpair&)) < minx#) THEN LET minx# =
VAL(x$(numbercurrentpair&))
                                IF (VAL(x$(numbercurrentpair&)) > maxx#) THEN LET maxx# =
VAL(x$(numbercurrentpair&))
                        END IF
                END IF
        LOOP
        CLOSE #3
        IF nodatapairs& >= minnum& AND nodatapairs& <= maxnum& AND (maxx# - minx#) >=
minrange# AND (maxx# - minx#) <= maxrange# THEN
                LET iteration# = iteration# + 1
                'OPEN "all_reg.tmp" FOR INPUT AS #3
                LET nodatapairscheck& = 0
                DO UNTIL nodatapairscheck& = nodatapairs&
                        '
                        'INPUT #3, x$, y$
                        LET nodatapairscheck& = nodatapairscheck& + 1
                        '
                        'this next bit is part of the calculations for the
                        'standard deviations of x and y
                        '
                        LET sumdevx# = sumdevx# + ((VAL(xtemp$(nodatapairscheck&)) - (sumx# /
nodatapairs&)) ^ 2)
                        LET sumdevy# = sumdevy# + ((VAL(ytemp$(nodatapairscheck&)) - (sumy# /
nodatapairs&)) ^ 2)
                LOOP
                'CLOSE #3
                '
                'The next bits calculate the standard deviations of x and y
                '
                LET stdevx# = (1 / (nodatapairs& - 1)) * sumdevx#
                LET stdevy# = (1 / (nodatapairs& - 1)) * sumdevy#
                '
                'The next bits calculate the variances of x and y
                '
                LET varx# = stdevx# ^ (.5)
                LET vary# = stdevy# ^ (.5)
                '
                'PRINT
                'PRINT
                '
                'the next lines calculate the slope and intercept of the regression,
respectively
                '
                LET slope# = (sumxy# - ((1 / nodatapairs&) * sumx# * sumy#)) / (sumx2# - ((1 /
nodatapairs&) * (sumx# ^ 2)))
                LET intercept# = (sumy# / nodatapairs&) - (slope# * (sumx# / nodatapairs&))
                '
                'This is an error checking routine
                IF stdevx# = 0 THEN PRINT " Probable divide by zero error: st dev x = ";
stdevx#
```

```
                IF stdevy# = 0 THEN PRINT " Probable divide by zero error: st dev y = ";
stdevy#
                IF stdevx# = 0 THEN PRINT " (sum xi - xbar)^2 = "; sumdevx#
                IF stdevy# = 0 THEN PRINT " (sum xi - xbar)^2 = "; sumdevy#
                IF stdevx# = 0 OR stdevy# = 0 THEN END
                '
                'the next line calculates the Pearson correlation coefficient (r) of the
regression
                '
                LET pearsonr# = (sumxy# - ((1 / nodatapairs&) * sumx# * sumy#)) /
((nodatapairs& - 1) * varx# * vary#)
                LET rsquared# = pearsonr# ^ 2
                '
                IF pearsonr# > 1 THEN
                        PRINT
                        PRINT " Oh No!!!, Something is wrong - The Pearson correlation
coefficient is greater than 1"
                        END
                END IF
                '
                'These line will display various calculation outputs
                'PRINT
                'PRINT
                'PRINT " Sum xy:", sumxy#
                'PRINT " Sum x:", sumx#
                'PRINT " Sum y:", sumy#
                'PRINT " Sum x-sq:", sumx2#
                'PRINT
                'PRINT " Iteration number:", iteration#
                'PRINT " Number of x- and y- pairs in whole file:", n&
                'PRINT " Number of data pairs in current subset:", nodatapairs&
                'PRINT
                'PRINT " The slope of the regression is:", slope#
                'PRINT " The y-intercept of the regression is:", intercept#
                'PRINT " The Pearson correlation coefficient (r)"
                'PRINT "        of the regression is:", pearsonr#
                'PRINT " The r-squared of the regression is:", rsquared#
                '
                PRINT #2, nodatapairs&; ","; (maxx# - minx#); ","; minx#; ","; ((maxx# +
minx#) / 2); ","; maxx#; ","; slope#; ","; intercept#; ","; rsquared#
                'LET nout&(iteration#) = nodatapairs&
                'LET rangeout#(iteration#) = (maxx# - minx#)
                'LET slopeout#(iteration#) = slope#
                'LET intout#(iteration#) = intercept#
                'LET r2out#(iteration#) = rsquared#
                CLOSE #1

        END IF
        LET current$ = TIME$
        LET currentss& = VAL(RIGHT$(current$, 2))
        DO UNTIL (currentss& - lastss&) >= 0
                LET lastss& = lastss& - 60
        LOOP
        IF currentss& > lastss& THEN
                GOSUB timecounter
                GOSUB totaltime
        END IF
        CLOSE #1
LOOP
CLOSE #1
GOSUB timecounter
'PRINT
'PRINT " Writing Results to file"
'FOR i = 1 TO numofiterations#
        'PRINT #2, nout&(i); ","; rangeout#(i); ","; slopeout#(i); ","; intout#(i); ",";
r2out#(i)
'NEXT i
CLOSE #2
GOSUB totaltime
SLEEP
END
'
timecounter:
LET clockerror& = 0
CLS
LET current$ = TIME$
LET currenthh& = VAL(LEFT$(current$, 2))
```

```
LET currentmm& = VAL(MID$(current$, 4, 2))
LET currentss& = VAL(RIGHT$(current$, 2))
DO UNTIL (currentss& - lastss&) >= 0
        LET lastss& = lastss& - 60
LOOP
LET sspast& = sspast& + (currentss& - lastss&)
PRINT
PRINT " Least-Squares Linear Regression Analysis of "; in$
PRINT
PRINT " Data sets will contain"; minnum&; "-"; maxnum&; "data pairs"
PRINT
PRINT " x-value range will be"; minrange#; "-"; maxrange#
'
IF iteration# > 3 THEN
        LET ssperloop# = sspast& / iteration#
        LET ssremaining# = (numofiterations# - iteration#) * ssperloop#
        LET hhremaining# = ssremaining# / (60 * 60)
        LET hhrem& = INT(hhremaining#)
        IF hhrem& > hhremaining# THEN LET hhrem& = hhrem& - 1
        LET ssremaining# = ssremaining# - (60 * 60 * hhrem&)
        LET mmremaining# = ssremaining# / 60
        LET mmrem& = INT(mmremaining#)
        IF mmrem& > mmremaining# THEN LET mmrem& = mmrem& - 1
        LET ssremaining# = ssremaining# - (60 * mmrem&)
        LET ssrem& = INT(ssremaining#)
        IF ssrem& > ssremaining# THEN LET ssrem& = ssrem& - 1
ELSEIF iteration# <> 0 THEN
        LET ssrem& = ssrem& - (currentss& - lastss&)
        IF ssrem& < 0 THEN
                LET ssrem& = ssrem& + 60
                LET mmrem& = mmrem& - 1
        END IF
        IF mmrem& < 0 THEN
                LET mmrem& = mmrem& + 60
                LET hhrem& = hhrem& - 1
        END IF
        IF hhrem& < 0 THEN LET clockerror& = 1
END IF
IF iteration# <= 3 THEN
        PRINT
        PRINT " Awaiting acceptance of the first four iterations"
        PRINT ; " "; (totaliterationsperformed&); "iterations have been processed, but failed
to meet acceptance criteria"
        IF iteration# = 1 THEN
                PRINT ; " "; iteration#; "has been accepted"
        ELSE
                PRINT ; " "; iteration#; "have been accepted"
        END IF
ELSE
        PRINT
        PRINT " Total iterations performed:"; totaliterationsperformed&
        PRINT " Number of iterations rejected:"; (totaliterationsperformed& - iteration#)
        PRINT " Processing accepted iteration number"; iteration#; "of"; numofiterations#
        IF sspast& < 30 THEN
                PRINT
                PRINT " An estimate of processing time will be available in"; (30 - sspast&);
"seconds"
        ELSEIF clockerror& <> 1 THEN
                PRINT
                PRINT " Estimated time remaining: "; hhrem&; "h  "; mmrem&; "min  "; ssrem&;
"s"
                PRINT
                PRINT " On average, data set selection takes"; (INT(1000 * ssperloop#)) /
1000; "seconds"
        END IF
END IF
LET lastss& = currentss&
LET lastiteration# = iteration#
RETURN
'
totaltime:
IF counter& = 1 THEN
        LET ssgone# = sspast&
        LET hhgone# = ssgone# / (60 * 60)
        LET hhg& = INT(hhgone#)
        IF hhg& > hhgone# THEN LET hhg& = hhg& - 1
        LET ssgone# = ssgone# - (60 * 60 * hhg&)
```

```
        LET mmgone# = ssgone# / 60
        LET mmg& = INT(mmgone#)
        IF mmg& > mmgone# THEN LET mmg& = mmg& - 1
        LET ssgone# = ssgone# - (60 * mmg&)
        LET ssg& = INT(ssgone#)
        IF ssrem& > ssremaining# THEN LET ssrem& = ssrem& - 1
        PRINT
        PRINT " Total Processing Time: "; hhg&; "h  "; mmg&; "min  "; ssg&; "s"
END IF
RETURN

SUB Large (in$, out$)
LET n& = 0
OPEN in$ FOR INPUT AS #1
DO WHILE NOT EOF(1)
        INPUT #1, x$, y$
        LET n& = n& + 1
        IF n& = 1 THEN
                LET minx# = VAL(x$)
                LET maxx# = VAL(x$)
        ELSE
                IF (VAL(x$) < minx#) THEN LET minx# = VAL(x$)
                IF (VAL(x$) > maxx#) THEN LET maxx# = VAL(x$)
        END IF
LOOP
CLOSE #1
'
TwoBackTheTruckUp:
CLS
PRINT
INPUT ; " How many sub-sample iterations do you wish to perform"; numofiterations#
IF numofiterations# < 1 THEN GOTO TwoBackTheTruckUp
PRINT
'DIM nout&(numofiterations#), rangeout#(numofiterations#), slopeout#(numofiterations#),
intout#(numofiterations#), r2out#(numofiterations#)
PRINT
'
PRINT , " "; in$; " contains"; n&; "x and y pairs"
PRINT
'
twohowmanysamples:
PRINT " What is the minimum number of x/y pairs that you would"
INPUT ; "   like the randomly selected subsets to contain"; minnum&
IF minnum& < 3 THEN
        PRINT
        PRINT
        PRINT " This program can not perform regression analysis on data subsets"
        PRINT " containing fewer than 3 values due to problems encountered during"
        PRINT " calculation of r-squared values"
        PRINT
        PRINT " Please re-enter"
        GOTO twohowmanysamples
END IF
PRINT
PRINT
PRINT " What is the maximum number of x/y pairs that you would"
PRINT "   like the randomly selected subsets to contain?"
PRINT "      Enter a number above the number of pairs in your"
INPUT ; "      data file to set no upper limit ", maxnum&
IF maxnum& > n& THEN LET maxnum& = n&
PRINT
PRINT
PRINT " Your data file has a total x-range of"; (maxx# - minx#)
PRINT " What is the minimum range between max and min x-values that you would"
INPUT ; "   like the randomly selected subsets to contain"; minrange#
PRINT
PRINT
PRINT " What is the maximum range between max and min x-values that you would"
PRINT "   like the randomly selected subsets to contain?"
INPUT ; "   Enter a number above the range of your data set to set no upper limit"; maxrange#
PRINT
PRINT
INPUT ; " Would you like a running estimate of remaining processing time"; counter$
IF counter$ = "y" THEN LET counter& = 1 ELSE LET counter& = 0
'
TwoCommence:
PRINT
```

```
PRINT
PRINT " Because of the large size of the input data file, this program will have"
PRINT " to frequently access the hard drive.  This will result in the loss of"
PRINT " considerable performance!"
PRINT
PRINT " Do you wish to commence calculations"
INPUT " (n to quit, so to start over, y to continue)"; start$
IF start$ = "n" THEN END
IF start$ = "so" THEN GOTO TheSubEnd
IF start$ = "y" THEN GOTO TwoCarryOn ELSE GOTO TwoCommence
'
TwoCarryOn:
'this bit takes a note of when the program started running
LET start$ = TIME$
LET starthh& = VAL(LEFT$(start$, 2))
LET startmm& = VAL(MID$(start$, 4, 2))
LET startss& = VAL(RIGHT$(start$, 2))
LET hhpast& = 0
LET mmpast& = 0
LET sspast& = 0
LET cumulativess& = 0
LET lastss& = startss&
LET totaliterationsperformed& = 0
LET clockerror& = 0
'
'this bit selects the random number list to use.  This is done using the
'system time as a changing base
RANDOMIZE (startss& * starthh& * startmm&)
'
'this bit randomly generates subsets of the entire data set
LET iteration# = 0
LET lastiteration# = 0
DO UNTIL iteration# = numofiterations#
Twoiteration:
        IF iteration# = 10000 * (INT(iteration# / 10000)) THEN RANDOMIZE (currentss& *
currenthh& * currentmm&)
        '
        LET totaliterationsperformed& = totaliterationsperformed& + 1
        '
        CONST false = 0, true = NOT false
        LET done = false
        LET sumxy# = 0
        LET sumx# = 0
        LET sumy# = 0
        LET sumx2# = 0
        LET sumdevx# = 0
        LET sumdevy# = 0
        LET numbercurrentpair& = 0
        LET nodatapairs& = 0
        '
        LET rejectlev# = RND
        '
        'This creates a temporary file where each new subset will be stored
        'for use in correlation coefficient calculations
        OPEN "all_reg.tmp" FOR OUTPUT AS #3
        '
        'This next bit will loop until it reaches the end of file 1 (EOF(1))
        OPEN in$ FOR INPUT AS #1
        DO UNTIL EOF(1)
                '
                LET numbercurrentpair& = numbercurrentpair& + 1
                '
                LET rand# = RND
                INPUT #1, x$, y$
                IF rand# >= rejectlev# THEN
                        'this counts the number of pairs in the current subset
                        LET nodatapairs& = nodatapairs& + 1
                        '
                        PRINT #3, x$, ",", y$
                        '
                        'this next bit is part of the regression calulation
                        LET sumxy# = sumxy# + (VAL(x$) * VAL(y$))
                        LET sumx# = sumx# + VAL(x$)
                        LET sumy# = sumy# + VAL(y$)
                        LET sumx2# = sumx2# + ((VAL(x$)) ^ 2)
                        '
                        IF nodatapairs& > maxnum& THEN
```

```
                                CLOSE #1
                                CLOSE #3
                                LET current$ = TIME$
                                LET currentss& = VAL(RIGHT$(current$, 2))
                                DO UNTIL (currentss& - lastss&) >= 0
                                        LET lastss& = lastss& - 60
                                LOOP
                                IF currentss& > lastss& THEN
                                        GOSUB Twotimecounter
                                        GOSUB Twototaltime
                                END IF
                                GOTO Twoiteration
                        END IF
                        IF (nodatapairs& + (n& - numbercurrentpair&)) < minnum& THEN
                                CLOSE #1
                                CLOSE #3
                                LET current$ = TIME$
                                LET currentss& = VAL(RIGHT$(current$, 2))
                                DO UNTIL (currentss& - lastss&) >= 0
                                        LET lastss& = lastss& - 60
                                LOOP
                                IF currentss& > lastss& THEN
                                        GOSUB Twotimecounter
                                        GOSUB Twototaltime
                                END IF
                                GOTO Twoiteration
                        END IF
                        '
                        IF nodatapairs& = 1 THEN
                                LET minx# = VAL(x$)
                                LET maxx# = VAL(x$)
                        ELSE
                                IF (VAL(x$) < minx#) THEN LET minx# = VAL(x$)
                                IF (VAL(x$) > maxx#) THEN LET maxx# = VAL(x$)
                        END IF
                END IF
        LOOP
        CLOSE #3
        IF nodatapairs& >= minnum& AND nodatapairs& <= maxnum& AND (maxx# - minx#) >=
minrange# AND (maxx# - minx#) <= maxrange# THEN
                LET iteration# = iteration# + 1
                OPEN "all_reg.tmp" FOR INPUT AS #3
                LET nodatapairscheck& = 0
                DO UNTIL EOF(3)
                        INPUT #3, x$, y$
                        LET nodatapairscheck& = nodatapairscheck& + 1
                        '
                        'this next bit is part of the calculations for the
                        'standard deviations of x and y
                        '
                        LET sumdevx# = sumdevx# + ((VAL(x$) - (sumx# / nodatapairs&)) ^ 2)
                        LET sumdevy# = sumdevy# + ((VAL(y$) - (sumy# / nodatapairs&)) ^ 2)
                LOOP
                CLOSE #3
                '
                'The next bits calculate the standard deviations of x and y
                '
                LET stdevx# = (1 / (nodatapairs& - 1)) * sumdevx#
                LET stdevy# = (1 / (nodatapairs& - 1)) * sumdevy#
                '
                'The next bits caculate the variances of x and y
                '
                LET varx# = stdevx# ^ (.5)
                LET vary# = stdevy# ^ (.5)
                '
                'PRINT
                'PRINT
                '
                'the next lines calculate the slope and intercept of the regression,
respectively
                '
                LET slope# = (sumxy# - ((1 / nodatapairs&) * sumx# * sumy#)) / (sumx2# - ((1 /
nodatapairs&) * (sumx# ^ 2)))
                LET intercept# = (sumy# / nodatapairs&) - (slope# * (sumx# / nodatapairs&))
                '
                'This is an error checking routine
```

```
                IF stdevx# = 0 THEN PRINT " Probable divide by zero error: st dev x = ";
stdevx#
                IF stdevy# = 0 THEN PRINT " Probable divide by zero error: st dev y = ";
stdevy#
                IF stdevx# = 0 THEN PRINT " (sum xi - xbar)^2 = "; sumdevx#
                IF stdevy# = 0 THEN PRINT " (sum xi - xbar)^2 = "; sumdevy#
                IF stdevx# = 0 OR stdevy# = 0 THEN END
                '
                'the next line calculates the Pearson correlation coefficient (r) of the
regression
                '
                LET pearsonr# = (sumxy# - ((1 / nodatapairs&) * sumx# * sumy#)) /
((nodatapairs& - 1) * varx# * vary#)
                LET rsquared# = pearsonr# ^ 2
                '
                IF pearsonr# > 1 THEN
                        PRINT
                        PRINT " Oh No!!!, Something is wrong - The Pearson correlation
coefficient is greater than 1"
                        END
                END IF
                '
                'These line will display various calculation outputs
                'PRINT
                'PRINT
                'PRINT " Sum xy:", sumxy#
                'PRINT " Sum x:", sumx#
                'PRINT " Sum y:", sumy#
                'PRINT " Sum x-sq:", sumx2#
                'PRINT
                'PRINT " Iteration number:", iteration#
                'PRINT " Number of x- and y- pairs in whole file:", n&
                'PRINT " Number of data pairs in current subset:", nodatapairs&
                'PRINT
                'PRINT " The slope of the regression is:", slope#
                'PRINT " The y-intercept of the regression is:", intercept#
                'PRINT " The Pearson correlation coefficient (r)"
                'PRINT "        of the regression is:", pearsonr#
                'PRINT " The r-squared of the regression is:", rsquared#
                '
                PRINT #2, nodatapairs&; ","; (maxx# - minx#); ","; minx#; ","; ((maxx# +
minx#) / 2); ","; maxx#; ","; slope#; ","; intercept#; ","; rsquared#
                'LET nout&(iteration#) = nodatapairs&
                'LET rangeout#(iteration#) = (maxx# - minx#)
                'LET slopeout#(iteration#) = slope#
                'LET intout#(iteration#) = intercept#
                'LET r2out#(iteration#) = rsquared#
                CLOSE #1

        END IF
        LET current$ = TIME$
        LET currentss& = VAL(RIGHT$(current$, 2))
        DO UNTIL (currentss& - lastss&) >= 0
                LET lastss& = lastss& - 60
        LOOP
        IF currentss& > lastss& THEN
                GOSUB Twotimecounter
                GOSUB Twototaltime
        END IF
        CLOSE #1
LOOP
CLOSE #1
GOSUB Twotimecounter
'PRINT
'PRINT " Writing Results to file"
'FOR i = 1 TO numofiterations#
        'PRINT #2, nout&(i); ","; rangeout#(i); ","; slopeout#(i); ","; intout#(i); ",";
r2out#(i)
'NEXT i
CLOSE #2
GOSUB Twototaltime
SLEEP
END
'
Twotimecounter:
LET current$ = TIME$
LET currenthh& = VAL(LEFT$(current$, 2))
```

```
LET currentmm& = VAL(MID$(current$, 4, 2))
LET currentss& = VAL(RIGHT$(current$, 2))
DO UNTIL (currentss& - lastss&) >= 0
        LET lastss& = lastss& - 60
LOOP
LET sspast& = sspast& + (currentss& - lastss&)
LET clockerror& = 0
CLS
PRINT
PRINT " Least-Squares Linear Regression Analysis of "; in$
PRINT
PRINT " Data sets will contain"; minnum&; "-"; maxnum&; "data pairs"
PRINT
PRINT " x-value range will be"; minrange#; "-"; maxrange#
'
IF iteration# > 3 THEN
        LET ssperloop# = sspast& / iteration#
        LET ssremaining# = (numofiterations# - iteration#) * ssperloop#
        LET hhremaining# = ssremaining# / (60 * 60)
        LET hhrem& = INT(hhremaining#)
        IF hhrem& > hhremaining# THEN LET hhrem& = hhrem& - 1
        LET ssremaining# = ssremaining# - (60 * 60 * hhrem&)
        LET mmremaining# = ssremaining# / 60
        LET mmrem& = INT(mmremaining#)
        IF mmrem& > mmremaining# THEN LET mmrem& = mmrem& - 1
        LET ssremaining# = ssremaining# - (60 * mmrem&)
        LET ssrem& = INT(ssremaining#)
        IF ssrem& > ssremaining# THEN LET ssrem& = ssrem& - 1
ELSEIF iteration# <> 0 THEN
        LET ssrem& = ssrem& - (currentss& - lastss&)
        IF ssrem& < 0 THEN
                LET ssrem& = ssrem& + 60
                LET mmrem& = mmrem& - 1
        END IF
        IF mmrem& < 0 THEN
                LET mmrem& = mmrem& + 60
                LET hhrem& = hhrem& - 1
        END IF
        IF hhrem& < 0 THEN LET clockerror& = 1
END IF
IF iteration# <= 3 THEN
        PRINT
        PRINT " Awaiting acceptance of the first four iterations"
        PRINT ; " "; (totaliterationsperformed&); "iterations have been processed, but failed
to meet acceptance criteria"
        IF iteration# = 1 THEN
                PRINT ; " "; iteration#; "has been accepted"
        ELSE
                PRINT ; " "; iteration#; "have been accepted"
        END IF
ELSE
        PRINT
        PRINT " Total iterations performed:"; totaliterationsperformed&
        PRINT " Number of iterations rejected:"; (totaliterationsperformed& - iteration#)
        PRINT " Processing accepted iteration number"; iteration#; "of"; numofiterations#
        IF sspast& < 30 THEN
                PRINT
                PRINT " An estimate of processing time will be available in"; (30 - sspast&);
"seconds"
        ELSEIF clockerror& <> 1 THEN
                PRINT
                PRINT " Estimated time remaining: "; hhrem&; "h  "; mmrem&; "min  "; ssrem&;
"s"
                PRINT
                PRINT " On average, data set selection takes"; (INT(1000 * ssperloop#)) /
1000; "seconds"
        END IF
END IF
LET lastss& = currentss&
LET lastiteration# = iteration#
RETURN
'
Twototaltime:
IF counter& = 1 THEN
        LET ssgone# = sspast&
        LET hhgone# = ssgone# / (60 * 60)
        LET hhg& = INT(hhgone#)
```

```
        IF hhg& > hhgone# THEN LET hhg& = hhg& - 1
        LET ssgone# = ssgone# - (60 * 60 * hhg&)
        LET mmgone# = ssgone# / 60
        LET mmg& = INT(mmgone#)
        IF mmg& > mmgone# THEN LET mmg& = mmg& - 1
        LET ssgone# = ssgone# - (60 * mmg&)
        LET ssg& = INT(ssgone#)
        IF ssrem& > ssremaining# THEN LET ssrem& = ssrem& - 1
        PRINT
        PRINT " Total Processing Time: "; hhg&; "h  "; mmg&; "min  "; ssg&; "s"
END IF
RETURN
'
TheSubEnd:
END SUB
```