

# Mass and Temperature Dependence of Metabolic Rate in Litter and Soil Invertebrates

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## ABSTRACT

Metabolic scaling theory provides a framework for modeling the combined mass and temperature dependence of metabolic rate. The theory predicts that whole-organism metabolic rate should scale with body mass raised to the 3/4 power as a consequence of the physical characteristics of internal distribution networks. Metabolic rate is predicted to vary with absolute body temperature,  $T$ , according to the Boltzmann factor,  $e^{-E/kT}$ , where  $E$  is the apparent activation energy of biochemical reactions, 0.2–1.2 eV, and  $k$  is Boltzmann's constant. I evaluated those predictions, using a compilation of published data on the metabolic rates of litter- and soil-dwelling earthworms, isopods, oribatid mites, springtails, and spiders. Earthworms, oribatid mites, springtails, and spiders had mass-scaling exponents that were statistically indistinguishable from the expected value of 0.75. The scaling exponent for terrestrial isopods, 0.91, was significantly greater than expected. All taxa had apparent activation energies within the predicted range of 0.2–1.2 eV. Activation energies for isopods, oribatid mites, springtails, and spiders were not significantly different from the average expected value of 0.6 eV, while the activation energy for earthworms, 0.25 eV, was significantly lower than 0.6 eV. Updated equations for estimating metabolic rate from body mass and environmental temperature are given for investigations into the ecological energetics of litter and soil animals.

## Introduction

Metabolic rate is the summation of matter and energy transformation rates within an individual organism. Metabolic rate determines the pace at which an organism grows and reproduces (McNab 1980; Ernest et al. 2003), interacts with members of its community (Brown et al. 2004), and exchanges matter and energy with the biosphere (Enquist et al. 2003; Allen et al. 2005). Metabolic rate also governs biological times such as the development time of individuals (Gillooly et al. 2002), time to competitive exclusion in communities (Brown et al. 2004), and the residence times of matter and energy in ecosystems (Allen et al. 2005). Because metabolic rate plays such an important role in biological processes occurring at multiple scales, factors that govern metabolic rates have become a subject of increasing interest to scientists from a wide variety of fields (Brown et al. 2004).

Of all variables known to influence metabolic rate, body mass and temperature are considered to be of primary importance. Historically, biologists have considered the effects of body mass and temperature separately. Mass has typically been considered in the context of allometry (Kleiber 1932; Hemmingen 1960), and temperature has usually been considered in a  $Q_{10}$  or Arrhenius equation framework (Van't Hoff 1896; Arrhenius 1915). Recent metabolic scaling theory has provided a synthetic framework for modeling the combined mass and temperature dependence of metabolic rate (Gillooly et al. 2001). The theory makes specific predictions, based on the nature of distribution networks (West et al. 1997; Banavar et al. 2002) and the thermodynamics of biochemical reactions (Gillooly et al. 2001), for how metabolic rate should vary with both body mass and temperature.

Predictions from metabolic scaling theory for the mass and temperature dependence of individual metabolic rate,  $B$ , follow from the equation

$$B = bM^{3/4}e^{-E/kT} \quad (1)$$

(Gillooly et al. 2001), where  $b$  is a taxon-specific normalization constant,  $M$  is body mass,  $e$  is the base of the natural logarithm,  $E$  is the apparent activation energy of biochemical reactions,  $k$  is Boltzmann's constant ( $8.62 \times 10^{-5}$  eV  $K^{-1}$ ), and  $T$  is body temperature (environmental temperature for ectotherms) in kelvins. This theoretical model can be linearized and evaluated using multiple-regression techniques. The linear form used in regression analysis is

$$\ln(B) = b_0 + b_1[\ln(M)] + b_2(1/kT), \quad (2)$$

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where  $b_0$  corresponds to the natural logarithm of  $b$  in equation (1);  $b_1$  corresponds to the scaling exponent for mass, which is expected to be 0.75; and the absolute value of  $b_2$  corresponds to the activation energy of biochemical reactions, which is expected to vary between 0.2 and 1.2 eV and average 0.6 eV (Gillooly et al. 2001).

Here, I consider the metabolic rates of litter and soil invertebrates (hereafter, soil invertebrates) in the context of metabolic scaling theory. I focus on soil invertebrates for two reasons. First, soil invertebrates play a critical role in decomposition and nutrient recycling (Phillipson 1971; Swift et al. 1979; Coleman et al. 2004). Thus, if human activities alter environmental temperature or the body mass distributions of soil invertebrates, then understanding the effects of these variables on invertebrate activity will be important for predicting changes in carbon balance and nutrient availability in ecosystems (e.g., Kirschbaum 1995; Allen et al. 2005). Second, studies evaluating metabolic scaling theory have included relatively few terrestrial invertebrates. Over the years, however, metabolic rate measurements have been conducted on many thousands of insects, arachnids, and oligochaetes. This accumulation of data offers an excellent opportunity to test theoretical predictions.

## Material and Methods

### *Data Acquisition*

I gathered data on metabolic rates for terrestrial isopods (Oniscoidea), earthworms (Oligochaeta), oribatid mites (Oribatida), springtails (Collembola), and spiders (Araneida) from the ecological energetics, animal physiology, and animal behavior literature. I excluded species from polar regions to reduce the possible effect of metabolic cold adaptation (Addo-Bediako et al. 2002) on the analysis. Hence, models and inferences from this study do not extend to polar invertebrates. I included spider taxa that were members of litter-dwelling families as described by Dondale (1990). A list of all taxa included in this analysis is provided in the appendix in the online edition of *Physiological and Biochemical Zoology*. The appendix contains currently accepted species names for isopods (Kensley et al. 2005), springtails (Bellinger et al. 2005), and spiders (Platnick 2005). The appendix contains species names from original metabolic rate publications for earthworms and mites because current global checklists are not readily available.

Metabolic rates of litter and soil animals were generally calculated from measurements of oxygen consumption. Oxygen consumption by microarthropods was measured using Cartesian driver or gradient driver respirometers (Petrušewicz and Macfadyen 1970). Oxygen consumption by larger invertebrates was measured with constant-pressure or constant-volume respirometers (Petrušewicz and Macfadyen 1970). In 0.02% of the cases, metabolic rates were calculated from measurements of carbon dioxide production by animals. Carbon dioxide measurements were made using gas chromatography (Mitchell

1973) or infrared gas analyzers (Lighton 1991). In the few cases where carbon dioxide production was reported, it was converted to an equivalent oxygen consumption value using an assumed respiratory quotient (RQ) of 0.82 (Petrušewicz and Macfadyen 1970). Oxygen consumption rates were then converted to metabolic rates ( $\text{J h}^{-1}$ ) using an oxyenergetic coefficient of  $20.20 \text{ J mL}^{-1} \text{ O}_2$ , which corresponds to an RQ of 0.82 (Prus 1975). The appendix contains all metabolic rate estimates used in this analysis. It is a simple task to convert between metabolic rates and oxygen consumption or carbon dioxide production rates using the RQ and oxyenergetic coefficient provided above.

The rates included in this analysis are a combination of standard metabolic rates (fasted, resting), resting metabolic rates (not fasted, resting), and minimum observed metabolic rates (possibly not fasted, nonactive to minimally active; IUPS 2001). Thus, many of the metabolic rate measurements in the data set do not represent the absolute lowest maintenance costs, as they may incorporate increases in metabolic rate due to the specific dynamic effect or occasional spontaneous activity of animals within respirometers. I did not include measurements of continuously active animals in the data set, for example, spiders measured while walking on treadmills.

The literature on soil invertebrate metabolism contains an abundance of intraspecific data on mass dependence but much less on temperature dependence. Thus, I adhered to the following rules for including data in this analysis. For each species in a study, I entered a single average metabolic rate for a single average body mass (mg). This often involved computing an average metabolic rate for a species using an average weight and an empirical, intraspecific allometric equation provided by the author. However, if a study included metabolic rate measurements for a species at multiple temperatures, I entered metabolic rate for an average mass for each level of temperature to maximize the amount of temperature information in the data set. If metabolic rates for a species were measured for animals of different sexes or at discrete developmental stages, I entered these measurements separately. Thus, the data set incorporates variation in metabolic rate due to mass, temperature, sex, and developmental stage to different degrees, depending on data availability.

### *Statistical Analysis*

There were two main objectives of this analysis. The first main objective was to generate a minimum set of predictive equations for estimating soil invertebrate metabolic rate from information on body mass and environmental temperature. The second objective was to compare the mass and temperature dependence of soil animal metabolism with predictions from metabolic scaling theory. To meet both of these objectives, it was necessary to determine whether mass and temperature dependence varied significantly across taxonomic group. I did this using general

linear models and analysis of variance. I began the analysis with the full data set and the interaction model

$$\ln(B) = b_0 + b_1[\ln(M)] + b_2(1/kT) + b_3(G) + b_4[\ln(M)G] + b_5[(1/kT)G]. \quad (3)$$

I used *F*-tests to test for significant interaction terms, which would indicate that mass and temperature slopes varied significantly across taxa in the full data set. If interaction terms were significant, I removed the taxa causing significant interactions and repeated the analysis. Once interaction terms were no longer significant, I removed them from the model and tested the taxon term, *G*, to determine whether intercepts were different across the remaining taxa. Finally, I repeated the process with the taxa that had been removed from the data set to determine whether model slopes and intercepts were different across those taxa.

Once I had a final set of metabolic rate models, I computed the confidence intervals (CIs) for model parameters. If 95% CIs for mass coefficients included 0.75 and those for temperature coefficients included values between  $-0.2$  and  $-1.2$  eV, then taxa incorporated in that model were determined to conform with theoretical predictions.

## Results

The data set compiled for this analysis included 420 metabolic rate estimates that were derived from more than 5,000 laboratory measurements and described in 62 publications (see appendix). Estimates were for 135 species in five broad taxonomic groups, which represented a wide range of trophic strategies and anatomical forms. Live-body masses ranged over several orders of magnitude, from  $1.70 \times 10^{-3}$  to  $1.05 \times 10^5$  mg. Temperature of metabolic rate measurements varied across the biologically relevant temperature range from  $-2^\circ$  to  $40^\circ\text{C}$ . Metabolic rate ranged over several orders of magnitude, from  $3.41 \times 10^{-6}$  to  $15.74 \text{ J h}^{-1}$ .

*F*-tests showed that taxon-mass and taxon-temperature interactions (eq. [3]) were statistically significant when all taxa were included in the data set (Table 1). This indicated that mass and temperature dependence varied across some of the taxa in

this study. When earthworms and isopods were removed from the data set, interaction terms were no longer significant (Table 1). When interaction terms were removed from equation (3) and the model was evaluated using data on mites, springtails, and spiders, the taxon term was found to be significant. This indicated that, although the mass and temperature dependence was similar across mites, springtails, and spiders, the overall mass- and temperature-corrected metabolic rate was different for at least one of the groups (Table 1). Finally, taxon-mass and taxon-temperature interaction terms were found to be significant when the full model was evaluated using data on earthworms and isopods, indicating that both the mass dependence and temperature dependence of metabolism varied significantly across these two taxa (Table 1).

Table 2 lists the minimum set of models for metabolic rate as indicated by the *F*-tests. One model is presented for earthworms, a second for isopods, and a third for mites, springtails, and spiders. The final model for earthworms ( $N = 28$ ,  $R^2 = 0.97$ ) had a mass slope of 0.71 (Fig. 1). The CI for the mass slope (0.66–0.758) included the theoretical value of 0.75. Thus, the mass dependence of earthworm metabolism was not distinguishable from that predicted by metabolic theory. The temperature slope (and 95% CI) for earthworms was  $-0.25$  eV ( $-0.32$  to  $-0.17$  eV; Fig. 2). The absolute value of this estimate fell within the expected range of 0.2–1.2 eV predicted by theory, although it was significantly lower than the average value of 0.6 eV.

The final model for isopods ( $N = 45$ ,  $R^2 = 0.90$ ) had a mass slope of 0.91. The CI for the mass slope (0.80–1.01) did not include the theoretical value of 0.75 (Fig. 1). Thus, the mass dependence of isopod metabolism was significantly higher than that predicted by metabolic theory. The temperature slope (and 95% CI) for isopods was  $-0.48$  eV ( $-0.61$  to  $-0.34$  eV; Fig. 2). The absolute value of this estimate fell within the expected range of 0.2–1.2 eV predicted by theory and was not significantly different from the average value of 0.6 eV.

The final model for oribatid mites, springtails, and spiders ( $N = 347$ ,  $R^2 = 0.98$ ) had a mass slope of 0.77. The CI for the mass slope (0.748–0.79) included the theoretical value of 0.75 (Fig. 1). Thus, the mass dependence of mite, springtail, and spider metabolism did not vary from that predicted by metabolic theory. The temperature slope (and 95% CI) for

Table 1: Summaries of *F*-tests for common slopes and intercepts across data sets with varying taxa

Data Set	Common Mass Slope			Common Temperature Slope			Common Intercept		
	<i>F</i>	df	<i>P</i>	<i>F</i>	df	<i>P</i>	<i>F</i>	df	<i>P</i>
All taxa	3.17	4, 405	.01	2.81	4, 405	.03			
Oribatid mites, springtails, and spiders	1.84	2, 338	.16	.60	2, 338	.55	195.63	2, 342	<.001
Springtails and spiders							1.70	1, 166	.19
Earthworms and isopods	8.84	1, 67	.004	5.22	1, 67	.03			

Table 2: Smallest set of predictive models for mass and temperature dependence of metabolic rate for selected litter and soil invertebrates

Taxon	$R^2$	Model for $\ln(\text{metabolic rate})^a$
Earthworms	.97	$5.70 + .71[\ln(\text{mass})] - .25[1/k(\text{temperature})]$
Terrestrial isopods	.90	$13.98 + .91[\ln(\text{mass})] - .48[1/k(\text{temperature})]$
Oribatid mites, springtails, and spiders <sup>b</sup>	.98	$18.42 - 1.36(\text{oribatids}) + .77[\ln(\text{mass})] - .58[1/k(\text{temperature})]$

<sup>a</sup> Metabolic rate is in joules per hour, live mass is in milligrams,  $k = 0.0000862$ , and temperature is in kelvins.

<sup>b</sup> In the equation, "oribatids" is an indicator variable with the value of 1 for oribatid mites and 0 for springtails and spiders.

mites, springtails, and spiders was  $-0.58 \text{ eV}$  ( $-0.64$  to  $-0.52 \text{ eV}$ ; Fig. 2). The absolute value of this estimate fell within the expected range of  $0.2\text{--}1.2 \text{ eV}$  predicted by theory and was not significantly different from the average value of  $0.6 \text{ eV}$ . The significant taxon term,  $-1.36(\text{oribatids})$ , where  $\text{oribatids} = 1$  for oribatid mites and  $0$  for springtails and spiders, indicated that oribatid mites, though they were similar in their mass and temperature dependence, had significantly lower ( $e^{1.36} = 3.9$  times lower) mass- and temperature-corrected metabolic rates than spiders and springtails.

**Discussion**

In the end, three models were necessary to predict the metabolic rates of the litter and soil invertebrates included in this study (Table 2). Individual models are reported for earthworms and isopods, while a single model is given for oribatid mites, springtails, and spiders. The models are suitable for coarse-grained studies of ecological energetics. Applications could include combining metabolic rate estimates with model predictions for production (Humphreys 1979; Ernest et al. 2003), lab estimates of

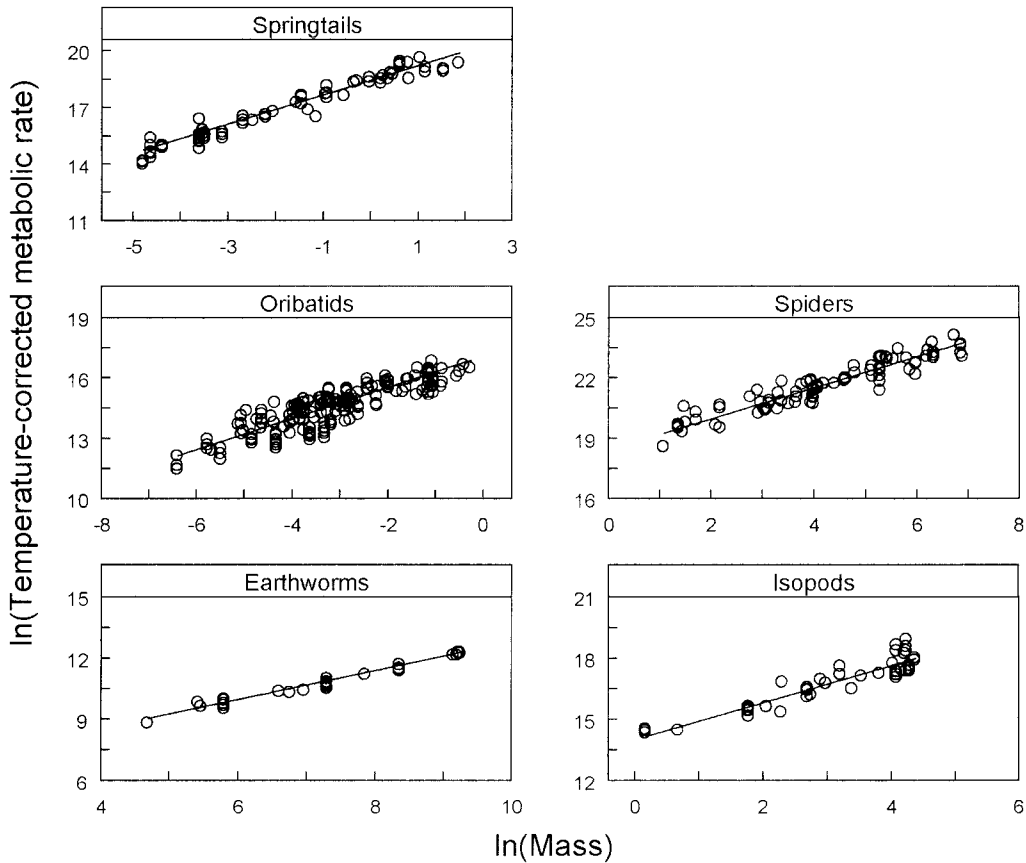


Figure 1. Mass dependence of metabolic rate for a variety of litter and soil invertebrates. Mass is the natural log of live body mass (mg). Metabolism is natural log-transformed and temperature-corrected by multiplying metabolic rate ( $\text{J h}^{-1}$ ) by  $e^{E/kT}$ , where  $E$  is the empirically determined activation energy of metabolism (eV), given as the temperature slope in Table 2;  $k$  is Boltzmann's constant ( $0.0000862 \text{ eV K}^{-1}$ ); and  $T$  is absolute temperature during metabolic rate measurements. Regression lines are derived from equations in Table 2.

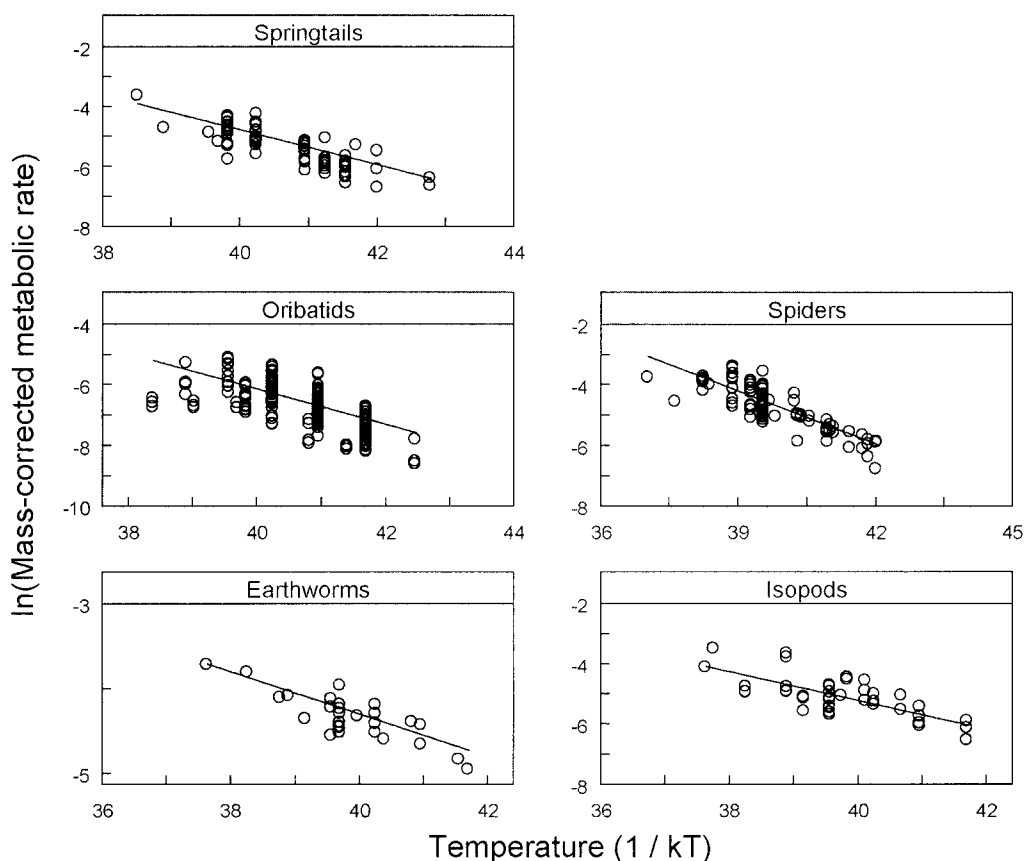


Figure 2. Temperature dependence of metabolic rate for a variety of litter and soil invertebrates. The X-axis shows the reciprocal of absolute temperature (K) during metabolic rate measurements multiplied by Boltzmann's constant ( $0.0000862 \text{ eV K}^{-1}$ ). Metabolism is natural log-transformed and mass-corrected by multiplying metabolic rate ( $\text{J h}^{-1}$ ) by live body mass (mg) raised to the empirically determined scaling exponent, given as the mass slope in Table 2. Regression lines are derived from equations in Table 2.

gestion (Petrušewicz and Macfadyen 1970), and field measurements of abundance (Phillipson 1971; Coleman et al. 1999) to estimate the direct contribution of soil invertebrate populations to energy flow in ecosystems. The models given in Table 2 could also be used to judge how energy flux through soil organisms might change in response to human alteration of environmental temperature (Kirschbaum 1995; Allen et al. 2005) and soil invertebrate body mass distributions (Allen et al. 2005).

Results from this analysis provide partial support for metabolic scaling theory. For example, for all taxa investigated, the temperature dependence of metabolism was not distinguishable from theoretical expectations. Also, in four of five taxa included in this study, the mass dependence of metabolism was not distinguishable from that predicted by theory. Importantly, however, the mass dependence of isopod metabolism was substantially greater than expected. This was a surprising result, given that intraspecific studies of isopod metabolism have reported mass-scaling exponents ranging from 0.68 for *Burmoniscus* sp. (Lam et al. 1991) to 0.83 for *Porcellionides pruinosus* (Al-Dabbagh and Marina 1986). The high mass dependence of isopod metabolism

could have come about for any number of biological or methodological reasons. It is worthy of further study, given that it suggests that organisms are able to circumvent fundamental constraints described by metabolic scaling theory.

The temperature dependence of earthworm metabolism, while within the range expected by theory, was significantly lower than the average value of 0.6 eV. The temperature dependence of earthworm metabolism has been a topic of curiosity for more than a century. Several investigators have found earthworm temperature dependence to be unusually low, with  $Q_{10}$  values being well below 2 and sometimes less than 1 (Vernon 1897; Abe and Buck 1985; Fitzpatrick et al. 1987; Chuang et al. 2004). This low temperature dependence has often been attributed to the earthworm's capacity for temperature acclimation within certain temperature ranges. Other studies have found the temperature dependence of earthworms to be on par with that of other animals (Pomeroy and Zarrow 1936) or have found evidence against temperature acclimation within temperature ranges above and below temperatures preferred by these animals (Fitzpatrick et al. 1987). The cellular-level mech-

animals involved in earthworm temperature acclimation are currently a subject of active research (Petersen and Holmstrup 2000; Crockett et al. 2001).

Finally, there are several aspects of this analysis that affect the applicability of the resulting models and the extent of the statistical inference. First, this analysis did not include animals from polar regions. Polar animals were excluded from the analysis in order to reduce the potential influence of metabolic cold adaptation (Addo-Bediako et al. 2002) on resulting models. The possible effect of metabolic cold adaptation on temperature dependence was not explicitly examined here because there were not enough data from polar animals across litter and soil taxa to justify complicating the analysis. Second, it should be noted that RQ values vary widely and depend on taxon, age, sex, activity, and season (Withers 1992). In order to include metabolic rate data from carbon dioxide measurements of animals, however, it was necessary to choose a standard RQ value. An RQ of 0.82 was chosen because it (1) represents utilization of a combination of lipids, proteins, and carbohydrates and (2) is commonly used in studies of ecological energetics (Petrusewicz and Macfadyen 1970). Note that when metabolic rates derived from carbon dioxide measurements were removed from this analysis, there were no changes in the conclusions of this study. Third, the data set used for this analysis frequently included multiple measurements from a given species, that is, measurements at multiple temperatures, from males and females, or from adults and immatures. Incorporating multiple measurements per species was done to maximize the information content of the data set in order to produce informed, predictive models for metabolic rate. However, this inclusive strategy could have introduced dependence among residuals and artificially reduced the breadth of CIs. Hence, the hypothesis tests related to metabolic theory should be interpreted with this in mind. Finally, the metabolic rate measurements used in this analysis were an opportunistic combination of standard metabolic rates, resting metabolic rates, and minimum observed metabolic rates (IUPS 2001). The relative proportions of these measurements in the data set are impossible to determine because, by definition, minimum observed metabolic rate measurements could include measurements of either standard or resting metabolic rates. Thus, the equations presented in Table 2 will not necessarily predict the absolute lowest energy requirements of animals. This should be kept in mind if factorial increases in metabolic rates are used to estimate energy expenditures of animals in the field (e.g., Albert 1983).

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