

Review

Field metabolic rate and body size

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Summary

The field metabolic rates (FMRs) of 229 species of terrestrial vertebrates, all measured using the doubly labeled water method in free-living individuals, were evaluated. Daily rates of energy expenditure were as low as 0.23 kJ per day in a small reptile (gecko), to as high as 52 500 kJ per day in a marine mammal (seal). This is a range of nearly six orders of magnitude. More than 70% of the variation in log-transformed data is due to variation in body size (expressed as body mass). Much of the remaining variation is accounted for by thermal physiology, with the endothermic mammals and birds having FMRs that are about 12 and 20 times higher, respectively, than FMRs of equivalent-sized, but ectothermic, reptiles. Variation in log(body mass) within each of these three taxonomic classes accounts for over 94% of the variation in log(FMR), and results from nonlinear regression analyses using untransformed data support this conclusion. However, the range of residual variation in mass-adjusted FMR within classes is still

more than sixfold (ratio of highest over lowest). Some of this variation is associated with affiliations with lower taxonomic levels (Infraclass: eutherian vs metatherian mammals; Family: passerine, procellariiform and galliform birds vs other birds), some is associated with habitat (especially desert vs nondesert), and some with differences in basic diet preference and foraging mode and season. The scaling slopes for FMR often differ from BMR slopes for the same Class of animals, and most differ from the theoretical slope of 0.75. Differences among slopes and intercepts that were detected using conventional regression analyses were largely confirmed upon reanalysis using Independent Contrasts Analysis to adjust for phylogenetic biases.

Key words: allometry, bird, doubly labeled water, ectothermy, endothermy, energetics, eutherian, FMR, mammal, metatherian, phylogeny, reptile, scaling coefficient.

Introduction

Perhaps the most essential resource needed by animals from their surroundings is energy. And probably the most important form of energy to animals is chemical potential energy in foodstuffs. This energy fuels living processes at every level of biological organization, and is considered to be the common currency of life. Thus, the primary goal of animals is to obtain sufficient food energy each day to satisfy daily needs. But what determines daily energy needs? We must know this in order to understand the mechanics underlying energetics of free-living animals, then to extrapolate it to an understanding of the impact of an individual on energy flow in its habitat, and also to predict the food requirements of animals in nature.

It is trivial to presume that bigger animals will have bigger energy needs than do smaller animals. But do size differences account completely for differences in daily energy needs? Or do other facets of the biology of animals, such as general life style (thermal physiology, diet, preferred habitat), ancestry (phylogeny), or environmental properties (season) have

important influences? In this review, the average field metabolic rates (FMRs) of species of three classes of terrestrial vertebrates (mammals, birds and reptiles) are examined in a search for the causes or correlates of variation in daily energy requirements. How large is the variation between species? Does variation in body mass completely account for variation in FMR? What other factors account for variation not explained by body mass differences alone? Do we know enough to make reliable predictions of daily energy and food requirements of vertebrates living in their natural habitats? Fortunately, reasonably satisfactory answers to these questions are available, and are summarized herein.

Field metabolic rate measurements

The discovery that isotopically labeled water could be used to measure the rate of carbon dioxide production in mammals (Lifson and McClintock, 1966) led to the use of the ‘doubly

labeled water' (DLW) method to measure FMR (in kJ metabolized per day) in a variety of vertebrate and invertebrate animals (Nagy, 1983a; Speakman, 1997). In an animal whose body water has been enriched with stable or radioactive isotopes of oxygen and hydrogen, the loss of hydrogen isotope over time is proportional to water flux through its body, but the loss of oxygen isotope is faster, because oxygen is lost not only as water, but also as CO₂ due to rapid isotopic equilibration in blood between H₂O and dissolved CO₂. Thus, the rate of CO₂ production can be estimated from the difference between the washout rates of the two isotopes, which represents CO₂ production only. Unfortunately, this method only works reliably in air-breathing animals, where a substantial fraction (around 15%) of the isotopic oxygen leaves the animal as CO₂. In water-breathing and amphibious animals, such as fishes and frogs, water molecules move through the animal so fast that they take out the oxygen isotope rapidly as water, and the now relatively small amount of oxygen isotope lost as CO₂ is difficult to detect and quantify accurately.

FMR values used in this review are for mammals (79 species), birds (95 species) and reptiles (55 species), as summarized by Nagy et al. (1999). More recent measurements on six additional species of marsupial mammals (Nagy and Bradshaw, 2000) were included in some statistical analyses. All FMR values (kJ day⁻¹) are means for a single species (from one or several studies averaged), with only one value per species being used. The results for birds are mostly for the breeding season, when labeled individuals could be recaptured reliably. Mammal data are for a variety of seasons, but reptile data represent the part of the year when these animals were abroad and active, not hibernating. Data were analyzed using a variety of methods, including conventional least-squares regression on log₁₀-transformed FMR and body mass values, nonlinear least-squares regression on untransformed data, analysis of variance, analysis of covariance, *t*-test, Mann-Whitney Rank sum tests (all using SigmaStat for Windows), and Independent Contrasts Analysis (Felsenstein, 1985) and PDTree (Garland et al., 1998) to adjust for phylogenetic biases.

Scaling of FMR

The lowest vertebrate FMR in the data set is 0.23 kJ day⁻¹ for a 3 g gecko in Africa, and the highest is 52 500 kJ day⁻¹ in harbor seals. This is a range of variation of over 200 000 times. Does variation in body mass account for all of this variation in FMR? Conventional allometric analysis, using log-transformed data in order to render the data into a straight line, yields a highly significant relationship ($P < 0.007$, $F_{1,227} = 547$) having the equation: $\text{FMR} = 2.25M_b^{0.808}$ (Fig. 1), where FMR is in kJ day⁻¹ and M_b is body mass in g. The r^2 value for this relationship is 0.707, indicating that about 71% of the variation in log(FMR) is due to variation in log(body size, expressed as body mass). Inspection of Fig. 1 indicates that the three vertebrate classes group somewhat differently, suggesting that separate regression analyses, at least for endotherms (birds

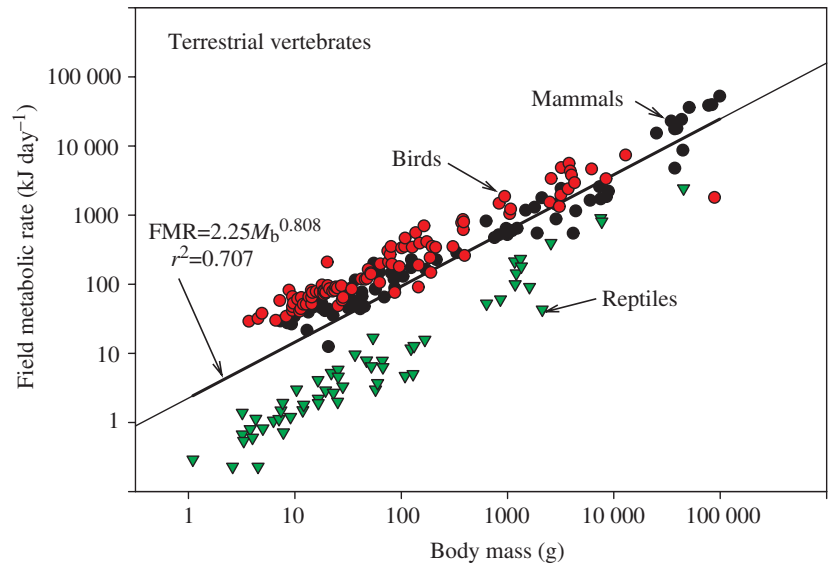
plus mammals) and ectotherms (reptiles) are warranted. These analyses yield better correlations: for endotherms, $\text{FMR} = 8.53M_b^{0.676}$, $N = 174$, $P < 0.001$, $r^2 = 0.915$, and for ectotherms (reptiles), $\text{FMR} = 0.196M_b^{0.889}$, $N = 55$, $P < 0.0001$, $r^2 = 0.945$. Thus, by accounting for thermal physiology first, body mass variation can explain 91–94% of variation in FMR (on a log–log basis). Further separation of endotherms into mammals and birds reveals even stronger body mass dependencies: for mammals, $\text{FMR} = 4.82M_b^{0.734}$, $N = 79$, $P < 0.0001$, $r^2 = 0.950$, and for birds, $\text{FMR} = 10.5M_b^{0.681}$, $N = 95$, $P < 0.0001$, $r^2 = 0.938$. So far, it appears that variation in FMR among terrestrial vertebrates is influenced most strongly by thermal physiology, then by (the closely correlated variable) taxonomic Class, then by body mass, such that within the Mammalia, Aves and Reptilia, log M_b variation accounts for 94–95% of the variation in log(FMR).

But the caveat that these conclusions refer only to the log-transformed data is worrisome. To address this drawback, the relationships were recalculated using a nonlinear regression method based on the model $\text{FMR} = aM_b^b$, where FMR = field metabolic rate in kJ day⁻¹, a = intercept, M_b = body mass in g and b = allometric slope. In general, the resulting r^2 values were similar to those above, indicating support for the conclusion that: variation in body mass accounts for most (90–95%) of the variation in FMR within Mammalia, Aves and Reptilia. However, the slopes and intercepts of the nonlinear regressions often differed substantially from those derived by conventional linear regression, but discussion of this phenomenon is beyond the scope of this review.

Remaining variation in FMR

The residual variation in FMR that is not explained by body mass is substantial, amounting to up to a sixfold range (ratio of maximum:minimum) in mass-adjusted values of kJ day⁻¹ (Nagy and Obst, 1991; Nagy, 1994). This means that, if FMR is predicted for a species on the basis of its Class and body mass alone, by using one of the linear equations reported above, the result can misrepresent the actual FMR of that species by as much as $\pm 70\%$ (that is, the real FMR may be as low as 30% of predicted or as high as 170% of predicted). What causes this residual variation, and can we account for it mathematically? By recalculating linear regressions for various subgroups, and by grouping residuals in a variety of ways, then testing for significant differences between groups, the following observations emerged. Regarding taxonomic effects below the Class level, marsupial mammals scale differently from eutherian mammals (slopes are 0.59 and 0.77, respectively), mainly because large marsupials (primarily macropods) have unusually low FMRs, and among bird families, Passeriformes and Procellariiformes have relatively high FMRs and Galliformes have relatively low FMRs. Regarding habitat effects, desert birds and desert eutherians have relatively low FMRs compared to their non-desert relatives, but desert lizards do not have unusually low FMRs. Also, marine birds have significantly higher FMRs than do

Fig. 1. Log-log relationship of field metabolic rate to body mass in 229 species of terrestrial vertebrates. The line is the least-squares regression for all the data. Mammal species are represented by filled circles, birds are shown with shaded circles and reptiles are indicated by shaded, inverted triangles. Sources of the data are given in full in Nagy (1987, 1994), Nagy and Obst (1991) and Nagy et al. (1999).



In summary: birds (Adams et al., 1987; Ambrose et al., 1996; Balance, 1995; Birt-Friesen et al., 1989; Brown et al., 1996; Bryant, 1997; Bryant and Westerterp, 1980; Bryant and Tatner, 1988; Bryant et al., 1984, 1985; Carlson et al., 1993; Castro et al., 1992; Chappell et al., 1993; Costa and Prince, 1987; Cuervo et al., 1996; Culik and Wilson, 1992; Dykstra and Karasov, 1993; Ellis et al., 1983; Fiala and Congdon, 1983; Flint and Nagy, 1984; Gabrielsen et al., 1987; Gales and Green, 1990; Gales et al., 1993; Gettinger et al., 1985; Goldstein and Nagy, 1985; Hails, 1979; Hails and Bryant, 1979; Hodum et al., 1998; Jonsson et al., 1996; Kam et al., 1987; Klaassen et al., 1992; Masman et al., 1988, 1989; Mehlum et al., 1993; Mock, 1991; Moreno, 1989; Moreno et al., 1988, 1991, 1995; Moreno and Sanz, 1996; Nagy et al., 1984, 1999; Nagy and Obst, 1992; Obst and Nagy, 1992; Obst et al., 1987, 1995; Pennycuick et al., 1990; Pettit et al., 1988; Piersma and Morrison, 1994; Powers and Conley, 1994; Powers and Nagy, 1988; Reyer and Westerterp, 1985; Ricklefs and Williams, 1984; Ricklefs et al., 1986; Riedstra et al., 1988; Roby and Ricklefs, 1986; Tatner, 1990; Tatner and Bryant, 1993; Tinbergen and Dietz, 1994; Utter and LeFebvre, 1973; Uttley et al., 1994; Vehrencamp et al., 1989; Ward, 1996; Weathers and Paton, 1997; Weathers et al., 1996; Weathers and Nagy, 1980; Weathers and Stiles, 1989; Weathers and Sullivan, 1993; Westerterp and Bryant, 1984; Williams, 1988a,b, 1993; Williams and Nagy, 1984, 1985; Williams et al., 1993, 1995; Williams and Du Plessis, 1996; Williams and Dwinell, 1990); mammals (Arnould et al., 1996; Bell et al., 1986; Berteaux et al., 1996; Bradshaw et al., 1994; Chevalier 1989; Costa and Gentry, 1986; Costa and Trillmich, 1988; Costa et al., 1985, 1989a, 1989b, 1990; Covell et al., 1996; Degen et al., 1986, 1991, 1992, 1997, 1998; Ellis et al., 1995; Foley et al., 1990; Geffen et al., 1992; Gettinger, 1984; Girard, 1998; Gorman et al., 1998; Green and Rowerowe, 1987; Green et al., 1989, 1991, 1992; Grenot et al., 1984; Hayes, 1989a,b; Helversen and Reyer, 1984; Holleman et al., 1982; Karasov, 1981; Kenagy et al., 1989; Krockenberger et al., 1998; Kunz et al., 1998; Kurta et al., 1987, 1989, 1990; Meerlo et al., 1997; Munger and Karasov, 1994; Monks and Green, 1995; Mullen, 1971a,b; Mullen and Chew, 1973; Mutze et al., 1991; Nagy et al., 1978, 1991; Nagy and Gruchacz, 1994; Nagy and Knight, 1994; Nagy and Martin, 1985; Nagy and Milton, 1979; Nagy and Montgomery, 1980; Nagy and Suckling, 1985; Nagy et al., 1990a,b, 1995; Peterson et al., 1976; Racey and Speakman, 1987; Randolph, 1980; Reilly and Fedak, 1991; Salsbury and Armitage, 1994; Seymour et al., 1998; Shoemaker et al., 1976; Smith et al., 1982; Speakman, 1997; Stephenson et al., 1994; Wallis and Green, 1992; Wallis et al., 1997; Williams et al., 1997); reptiles (Anderson and Karasov, 1981, 1988; Beaupre, 1996; Benabib and Congdon, 1992; Bennett and Nagy, 1977; Bickler and Nagy, 1980; Bradshaw et al., 1987; Brown and Perez-Mellado, 1994; Brown et al., 1992, 1999; Christian and Green, 1994; Christian et al., 1995, 1996a,b; Congdon and Tinkle 1982; Congdon et al., 1979; Dryden et al., 1990, 1992; Green et al., 1986, 1991a,b, 1997; Grenot et al., 1995; Henen, 1997; Karasov and Anderson, 1998; Kingsbury, 1995; Marler et al., 1995; Mautz and Nagy, 1987; Merker and Nagy, 1984; Nagy, 1982; Nagy and Bradshaw, 1995; Nagy and Degen, 1988; Nagy and Knight, 1989; Nagy and Medica, 1986; Nagy and Shoemaker, 1975, 1984; Nagy et al., 1984, 1991, 1993; Peterson, 1996; Peterson et al., 1998; Robinson, 1990; Secor and Nagy, 1994; Thompson et al., 1997; Van Marken Lichtenbelt et al., 1993; Vernet et al., 1988, 1995; Znari and Nagy, 1997).

non-marine species. Regarding diet specialization and foraging mode, carnivorous mammals scale differently (significantly higher slope; 0.85) than non-carnivore mammals, seed-eating birds (granivores) have relatively low FMRs, and widely foraging lizards have higher FMRs than do sit-and-wait (ambush) foraging lizards. (Basal metabolic rate in terrestrial vertebrates also varies with diet and other parameters; McNab, 1988.) Unfortunately, in spite of these significant influences on FMR, it does not appear that accounting for them is going to reduce the error in predicted FMR values below about twofold, or about $\pm 35\%$. This conclusion is based on the observation that r^2 values for several subgroups mentioned above are no higher than about 0.97 (table 2 in Nagy et al., 1999). It would be valuable to do a multiple regression analysis on currently available FMR

values, in order to explore the amount of unexplained variation in the data.

Allometric slopes

The scaling coefficients, or allometric slopes, of the conventional linear regressions are useful for several reasons. First, there are theoretical arguments suggesting that all FMR, BMR (basal) and SMR (standard) slopes should be either 0.67 or 0.75 (Savage et al., 2004; and see other studies in this volume). Second, if slopes for FMR are the same as for BMR within a taxon, predicting FMR from BMR becomes possible (FMR may be a constant multiple, say $3\times$, of BMR), allowing use of the much larger BMR database. Third, if FMR and BMR slopes differ, this can lead to discovery of unanticipated body

size effects in FMR. So, do FMR slopes all have values near either 0.67 or 0.75, and are FMR slopes the same as BMR slopes? Inspection of Fig. 2 indicates (1) that most FMR slopes (four out of six) differ significantly from 0.75, and (2) that in half of the taxa tested (two out of four), FMR and BMR slopes differ from each other. Thus, there is little support for the generalization that allometric slopes for FMR can be well represented by the value of 0.75, and even with a small sample size of four taxa, there is no trend in present data suggesting that FMR slopes are identical to BMR slopes.

Phylogenetic adjustment using Independent Contrasts Analysis

Some pairs of species, say dogs and wolves, are more closely related than are other pairs of species, say dogs and cats, but conventional regression analyses, both linear and nonlinear, involve the assumption that the data points are independent of each other. This assumption is violated in

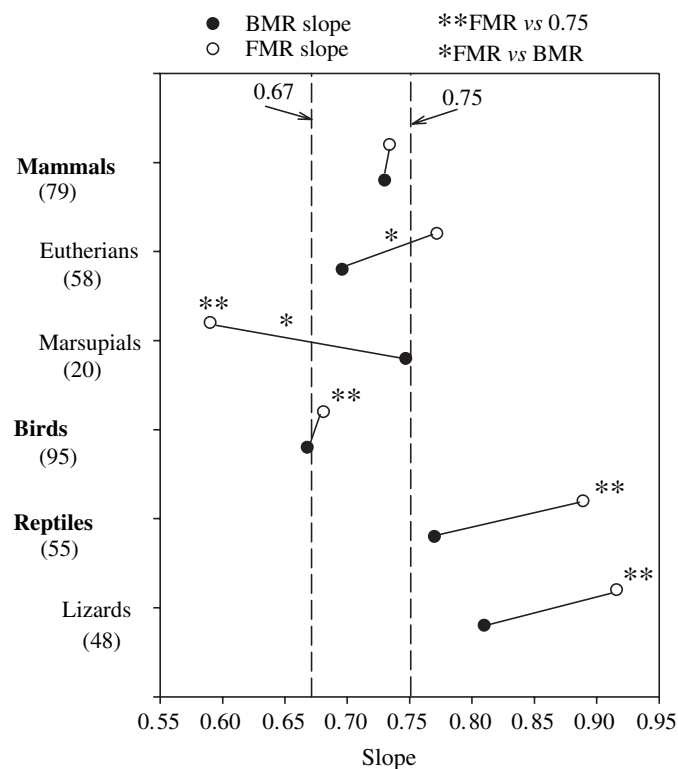


Fig. 2. Allometric (scaling) slopes, or b values, from linear regressions of log-transformed variables, for FMR (open circles) and BMR (or SMR for reptiles and lizards; filled circles), compared to the theoretical slopes of 0.67 and 0.75. **FMR slope for that taxon differs significantly from 0.75; *FMR and BMR for that taxon differ significantly from each other. Numbers of species included in the FMR slope calculations are shown in parentheses. BMR slopes (or SMR slopes for reptiles) are from Kleiber (1975; for mammals, eutherians), Hayssen and Lacy (1985; mammals, eutherians, marsupials), Dawson and Hulbert (1970; marsupials), Lasiewski and Dawson (1967; birds), and Bennett and Dawson (1976; reptiles, lizards).

datasets such as the FMR and body mass values analyzed in this review. Thus, a phylogenetic bias in the data may lead to incorrect statistical conclusions. The influence of phylogeny can be minimized by using ICA (Felsenstein, 1985; Garland et al., 1998). The allometric relationships described herein were reanalyzed using ICA (see details in Nagy et al., 1999) in order to evaluate this error source. Most slope and intercept values obtained from ICA were not significantly different from those obtained using conventional analyses. However, there were some potentially important differences in statistical conclusions between ICA and conventional analyses. For example, the significant difference in conventional slopes of passerine birds compared with birds other than passerines disappears upon reanalysis by ICA. In general, ICA identified fewer statistically significant differences than did conventional analyses, and ICA did not detect any new differences that were not already detected by conventional analyses. As more data become available and more refinements in ICA methods are made, the power and utility of ICA conclusions will increase, and it may become possible to use ICA exclusively to address the questions of the extent of dependence of FMR on body size, and the roles of other variables in determining FMR in vertebrate animals.

Annual FMR and food requirement

How does the yearly requirement for energy, or annual FMR, scale with body mass? Those people that work with wild animals, either in captivity or free-ranging, including conservation biologists, paleontologists, animal nutritionists and zookeepers, need to know the daily, monthly and annual energy and food demands of their species of interest. Predictive equations, all based on body mass as the most important variable, are available for daily FMR (Nagy et al., 1999) and daily food requirements (Nagy, 2001) of terrestrial vertebrates. The values for daily food needs of animals that were used in deriving these predictive allometric equations were estimated, from FMR, diet composition and digestibility data, as the consumption rate necessary to provide just that daily amount of metabolizable energy that was used in respiration. The r^2 values for these regressions are nearly as high or are higher than those for the FMR regressions. This supports the conclusion that daily food needs of free-ranging vertebrates, within taxonomic classes, are determined primarily by body size (mass). However, on a seasonal and annual basis, animals consume additional food, which provides the substances for growth and reproduction, and this additional food is not accounted for in the predictive equations that are currently available. It seems likely that intake rates of food that is allocated to growth should also be determined largely by body size, but such a relationship for wild vertebrates has yet to be supported by field measurements. This constraint, along with the caveat that most FMR measurements (and derived predictive equations) for birds are from breeding birds, should be kept in mind when applying the currently available allometric equations to

estimate annual food or energy requirements species of interest.

A few field studies have been through an entire year, and the results are instructive. The FMR of a small endotherm (desert kangaroo rat; Nagy and Gruchacz, 1994) was higher during winter, but the FMR of a small ectotherm (desert lizard; Nagy, 1983b), which is inactive in cold weather, was lowest in winter. So the effects of cold weather on endotherms and ectotherms are the opposite, in general. Thus, on an annual basis, the FMR (and food requirements) of an endotherm are likely to be around 30 times greater than those for an equivalent-sized ectotherm, much greater than the $15\times$ difference expected during the warm seasons. Endothermy is a very expensive life-style compared to ectothermy.

Conclusions

There are large differences in daily energy expenditures (FMRs) among equal-sized reptiles, birds and mammals. Within each of these taxonomic Classes, body size is the major determinant of daily energy and food requirements, accounting for about 95% of the variation present in currently available results. However, the remaining variation (up to sixfold) is substantial, and erodes the reliability of FMRs predicted on the basis of Class and body mass alone. Some of this residual variation is due to lower taxonomic affiliation, habitat, diet and foraging mode, but much of it remains unexplained. Allometric slopes for FMR range from 0.59 (marsupials, $N=20$ species) to 0.92 (lizards, $N=48$ species), and they differ from BMR slopes in half of the taxa tested, and from the theoretical slope of 0.75 in two thirds of the taxa tested. Independent Contrasts Analyses (ICA), used to account for phylogenetic biases, and non-linear regression analyses, used to avoid statistical conclusions relating only to log-transformed results, generally supported and confirmed the conclusions derived from conventional linear regression analyses done on log-transformed data. Preliminary evidence indicates that, on an annual basis, endothermy may cost an animal about thirty times more to fuel than if it operated itself as an ectotherm instead. The obvious success of endothermic vertebrates on this planet indicates that the astoundingly-expensive endothermic way of life confers large advantages over ectothermic vertebrates in getting and processing food at a high

rate. The mechanisms involved in this process remain to be elucidated.

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