BODY MASS AND BASAL METABOLISM OF
EXTINCT MAMMALS

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Abstract—1. Body mass and basal metabolic rate of extinct mammals are estimated by equations derived from the relationship between two skeletal measurements and body mass in extant mammals.
2. Accurate estimation of mass and basal metabolism allows the construction and testing of new hypotheses dealing with general scaling phenomena, organismal and faunal energetics, extinction, and community population dynamics.

INTRODUCTION

There is no direct way to measure the physiological responses of extinct mammals. However, if we accept the proposition that the cellular energetics of mammals have not changed since the initial evolution of endohomoiothermy, then we can extrapolate some physiological information for extinct mammals from relationships that exist among extant ones.

Basal metabolic rate \((M_b)\) in Kcal/day relates to body mass \((W)\) in kg in mammals as

\[
M_b = kW^{0.75}
\]

(1)

where \(k\) is a constant equal to 70. This equation describes the classic “mouse to elephant” curve of physiology, first analyzed in detail by Kleiber (1961). Text-equation (1) will be referred to as the Kleiber equation in subsequent discussion. Its mass-specific form is measured most often in \(\text{cc} O_2/\text{g} \cdot \text{hr}\) and is simply

\[
M_b/W = 3.4 W^{-0.25}
\]

(2)

where \(W\) is expressed in g.

If we accept a further assumption that correlations between skeletal measurements and body mass in extant mammals can be applied to extinct species, then it follows that a skeletal measurement can be used to predict basal metabolism. It need only be demonstrated that \(W\) can be accurately estimated by this measurement. In other words, if we construct an equation which takes the form \(W = kM_s\) where \(M_s\) equals some skeletal measurement, then substitution of the right side of the latter equation into text-equations (1) and (2) will allow estimation of \(M_b\) and \(M_b/W\).

For this study I chose two measurements, the greatest width across the occipital condyles (condylar width, \(C\)) and the greatest width across the head of the femur (femoral head width, \(F\)), which appeared intuitively to be related to body mass. These hypotheses were tested and accepted. It was also found that arvicoline rodents, weasels, and mammals < 100 g were lighter than was predicted by an equation relating masses of all mammals to condylar width. Separate equations were constructed that correct for these anomalies.

Recent papers by Iverson (1972) and McNab (1970, 1974, 1978a,b,c) have shown that the 0.75 power does not properly describe the relationship between \(M_b\) and \(W\) for certain mammalian species and size ranges. Shrews, arvicoline rodents, and weasels are notorious for demonstrating \(M_b\) higher than is predicted by mass (McNab, 1974; McManus, 1974) Sloths and marsupials less than 1 kg, on the other hand, demonstrate considerably lower metabolism than predicted. For convenience I have excluded sloths and smaller marsupials from this analysis. Separate equations relating metabolism to body mass were constructed for shrews, arvicoline rodents, and weasels. These equations were used in conjunction with the Kleiber equation to provide accurate estimates of metabolism in extant mammals. It was not my purpose in this manuscript to be exhaustive, either in number of species or individuals, but rather to create general equations for all mammals that provide predictions that can be expected to fall within species boundaries.

MATERIALS AND METHODS

Specimens

In addition to groups of specimens which allowed comparison between the two skeletal measurements, groups were created which allowed comparison between mass data derived solely from specimen tags (\(W_m\)) and those reported in the literature (\(W_l\)). Since few scientists are fortunate enough to have large collections of specimens with associated mass data available, the problem could be alleviated if it could be shown that average mass data as published in the literature could be used as estimators of mass in a given species in a bivariate plot of mass and some other parameter.

With the exception of measurements in Felis, which were taken from Kurtén (1965), \(C\) and \(F\) were measured on specimens in the vertebrate collections at Fairleigh Dickinson University (FDU). The following groups of specimens form the basis for the equations derived in this paper:

Body mass

Group IC. One adult chosen at random from each of 26 species. \(N = 26\). Condylar width is measured on each. Mass data are averages taken from the literature (McNab, 1963, 1970, 1974; Davis, 1966; Walker, 1975) only when estimates are unavailable from the other sources.
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Both are significantly different from the slope representing Group II specimens \( (P < 0.05) \). None of the equations are completely satisfactory for exact estimation of \( W \) in all mammal species or size ranges, but I have chosen that constructed from Group IC data for some further calculations. There is little statistical basis for this decision and the reader may prefer an equation derived from another group. Since the highest correlation exists between \( F \) and \( W \) \( (r = 0.99) \), Group II may appear to be the logical choice. However, complete skeletons with associated mass data are rare finds, and as a result the number of specimens is low. Nevertheless, these equations may be useful when cranial data are absent. The reader is cautioned to remember that additional equations should then be constructed for species less than 100 g and for weasels. Figure 2 presents a comparison of values of \( W \) estimated by equation (2) in Table 2 (from Group IC) with observed values.

Group II was chosen as a sort of "control" to Group IC, where only one adult specimen per species was measured, but \( W \) was available as tag data. However, I found that estimates of \( W \) generated by the Group II equation (No. 3 in Table 2) were occasionally too high for large mammals. This may be due to the fact that FDU specimens with associated mass data were under 1 kg.

It is interesting that Groups IC and III should generate essentially identical equations, since (a) mass data for Group IC derives solely from the literature \( (W_m) \) and mass data for Group III derives solely from specimen tags \( (W_n) \), and (b) the correlation between

Statistical and mathematical methods

Equations and straight lines relating body mass to \( C \) and \( F \), and \( M_b/W \) to \( W \) were constructed through least squares analysis of logarithmic data. Gould (1975) summarized the value of major axis versus least squares methods. I preferred to use the latter. Logarithmic expressions were converted to their exponential forms, and equations predicting \( M_b/W \) for (1) shrews and arvicoline rodents, (2) weasels, and (3) all other mammals were derived by substitution of equations solved for condylar width or femoral head width into those relating \( M_b/W \) to \( W \). As mentioned above, \( M_b/W \) data were then converted to \( M_b \) in Kcal/day.

RESULTS

I have chosen not to publish the exhaustive comparisons of mass and metabolic data generated by all the equations derived here. Rather, I have summarized my findings below and have gone on to use only those equations which provided satisfactory accuracy.

Body mass

As can be seen in Table 2 and Fig. 1, the equations derived from Group IC and III specimens are virtually identical. Statistical comparison of the slopes (powers) confirms this (Student’s \( t \)-test: \( P > 0.05 \)).
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Table 4. Equations that predict mass-specific metabolism in mammals

<table>
<thead>
<tr>
<th>Group</th>
<th>Species</th>
<th>Equation</th>
<th>r</th>
<th>Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Kleiber equation)</td>
<td>All mammals</td>
<td>$M/W = 3.4 W^{-0.25}$</td>
<td>—</td>
<td>(1)</td>
</tr>
<tr>
<td>VII</td>
<td>Shrews, arvicoline rodents, weasels</td>
<td>$M/W = 0.59 W^{-0.45}$</td>
<td>0.93</td>
<td>(2)</td>
</tr>
<tr>
<td>VIII</td>
<td>All mammals</td>
<td>$M/W = 2.27 C^{-0.75}$</td>
<td>—</td>
<td>(3)</td>
</tr>
<tr>
<td>IX</td>
<td>Mammals &gt; 100 g</td>
<td>$M/W = 7.60 C^{-0.93}$</td>
<td>—</td>
<td>(4)</td>
</tr>
<tr>
<td>IC</td>
<td>Shrews, arvicoline rodents</td>
<td>$M/W = 57.4 C^{-1.18}$</td>
<td>—</td>
<td>(5)</td>
</tr>
<tr>
<td>V</td>
<td>Weasels</td>
<td>$M/W = 457 C^{-1.39}$</td>
<td>—</td>
<td>(6)</td>
</tr>
</tbody>
</table>

$C$ and $W$ for Group IC specimens is much better ($r = 0.98$) than for Group III specimens ($r = 0.83$). We can conclude from (a) that, contrary to Gould (1973), mass data as published in the literature are accurate estimates of species mass. The lack of point variation in Group IC probably accounts for (b). The beneficence of observing four orders of magnitude corrects for this level of variation except in the case of arvicoline rodents, mammals less than 100 g, and weasels. Separate equations for these species (Groups IV-VI) are also presented in Table 2.

Estimates of body mass generated by equations (2), (5), and (6) in Table 2 are compared to $W_{av}$ and $W_{L}$ values in Table 3. Only the estimate for *Erethizon dorsatum* diverges significantly from average $W_{av}$ and $W_{L}$ values; it is too low. In this case (representing a single specimen) the animal is heavier than predicted by condylar width. Perhaps the inability of condylar width to accurately estimate mass in the porcupine is a reflection of a phenomenon inherent to hystricomorph rodents. Until such data are gathered, entering $C$ for *E. dorsatum* into the arvicoline equation provides a closer approximation (5.02 kg) to recorded average values of mass (7.90 kg).

Metabolism

Equations (3) and (4) in Table 4 were derived by substitution of equations (1) and (2) in Table 2 into the mass-specific form of the Kleiber equation (equation 1 in Table 4). Equations (5) and (6) in Table 4 were derived by substitution of equations (5) and (6) in Table 2 into an equation I derived in this study to describe the mass-specific basal metabolism of shrews, arvicoline rodents and weasels (equation 2 in Table 4). Separate equations with condylar width substituted for mass in shrews and arvicoline and weasels provided more accurate estimates of metabolism for most species than did the equation describing the three groups simultaneously.

Examination of the metabolic data in Table 3 and Fig. 3 shows that the derived equations provide accurate estimates of average basal metabolism for most species, both on a mass-specific and mass-dependent basis. Estimates for the opossum, *Didelphis virginiana*, are significantly higher than observed values, in spite of the relatively large size of this species. These data apparently reflect the general decrease of marsupial metabolic rates below those of placental mammals of comparable body mass (McNab, 1978b).

**DISCUSSION**

There is a variety of ways in which the equations presented here could have been derived and a variety of data that could have been used to generate these equations. I have labored on this topic in order to prove that reasonably accurate equations can be formed in any of these ways, given almost any combination of data, as long as sample sizes are satisfactory. I am particularly pleased with the result that allows published mass values to be used as species estimators of mass. Further research goals in theoretical paleobiology are now much more accessible.

Fig. 3. Relationship of mass-specific basal metabolic rate ($\text{ccO}_2/\text{g-hr}$) to body mass (kg) in all mammals as predicted by the mass-specific form of the Kleiber equation (K) and its derived form (C) using condylar width as an estimator of $W$, shrews and arvicoline rodents (S), and weasels (W). Lines (S) and (W) are derived from equation (2) in Table 4 using condylar width as an estimator of $W$. Solid circles = observed values, stars = additional observed arvicoline records from McNab (1973) and McManus (1974). 1 = *Sorex cinereus*, 2 = *Microtus pennsylvanicus*, 3 = *Blarina brevicauda*, 4 = *Mustela erminea*. 
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with which it was contemporaneous during the Late Pleistocene (Martin, 1974). Mass and metabolic data in Table 5 lend credence to the hypothesis that the Late Pleistocene carnivore megafauna preyed exclusively on large ungulate and sloth species.

Energetic relations can lead to useful hypotheses concerning extinction of taxa and modification of entire faunas. It is not sufficient merely to describe size change in an evolving lineage. The words large and small connote no causal ecological relationships in the absence of the physiological correlates of size: namely, mass, metabolic rate, conductance, body temperature, and energy consumption and expenditure. Large size was selected for in both cotton rats and horses (Martin, 1979), and it should be instructive to compare the energy relations of these groups through time with each other and with other mammalian species recovered from contemporaneous deposits. Is energy consumption stable through an evolving lineage, or can there be expected to be a net gain or loss? If there is a gain or loss, is it made up through extinction or recruitment of species with similar habitat preference and ecological requirements? With regard to entire faunas, these questions perhaps may lead to recognition of homeostatic (?) patterns through time. Are these patterns any different for glacial versus nonglacial periods? Biostratigraphic data have allowed the development of a fairly refined chronology of Pleistocene faunas in north Florida (Martin, 1974, 1978; Martin & Webb, 1974). It should be possible to use this progression of faunas as a model to test the feasibility of such questions.

Estimation of community dynamics often requires information regarding the number of individuals or standing crop biomass in an area. I have remained skeptical of the theoretical basis for both the older and newer “Shotwellian” approaches to the estimation of numbers or standing crop (see Shotwell, 1955; Kranz, 1977; Grayson, 1978), and would like to suggest an alternative model that appears to me to be on a much more sound theoretical foundation. McNab (1963) illustrated a correlation between home range and body mass in extinct mammals. Equations were constructed for all mammals and then specifically for “hunters” and “croppers”. If these equations accurately estimate home range then substitution of the mass-predicting equations in Table 2 into McNab’s equations will allow estimation of home range in extinct species. (Since publication of McNab’s equations more than 15 years ago a great deal of new home range information has become available. My preliminary calculations generate equations which differ somewhat from his. Whether they will be shown to be statistically different remains to be seen.) These data, when divided into a given geographic area will provide a minimum estimate of population size in that area. Once population size has been determined, the energetic impact of a mammalian fauna may be calculated. Theoretically then, energetic data from a progression of faunas will reveal the manner in which energy has been partitioned through time.

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REFERENCES


