Comparative Energetics of Gravity-muscle Interactions and Basal Metabolism

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Brody Memorial Lecture XVII

Special Report 298
October, 1982

Agricultural Experiment Station
University of Missouri-Columbia

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Comparative Energetics of Gravity-muscle Interactions and Basal Metabolism

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We celebrate the scientific works of Samuel Brody who, with Kleiber and Clark, firmly established a mathematical physiology for bioenergetics and growth. It was the philosopher Kant who declared that the chemistry of his day was a science but not Science, for the testing ground of true science is in its relationship to mathematics (Thompson, 1961). Those of us who have had the privilege of intellectual encounters with physical chemistry know how well VanHoft laid the firm foundations of the mathematical chemistry a hundred years later. Indeed, it is a tribute to the labors of Brody that we have so many mathematical expressions of those parabolas of energy utilization and growth for applied animal husbandry today.

It has been 50 years since Kleiber discovered the interspecies mean for metabolism in homeotherms. Almost immediately Brody and Procter (1932) published a similar result. Clark (1927) showed that the heart beat among animals could be standardized to $kW^{-.27}$. It is appropriate that we commemorate the semicentennial of the works of Brody and Kleiber with a new search for meaning in this broad spectrum equation that relates similarity in so many animals.

My interest in this subject arises from 20 years of teaching animal energetics, a year of research with Max Kleiber in Davis, California, and the appearance among recent physiological literature of absurd uses (Economos, 1979) and denial of metabolic size as a useful biological benchmark (Geer and Michels, 1982). Finally, the valuable applications of the equations of the parabolas of growth and metabolism in the new technology of animal feeding, the microprocessor and the minicomputer.

The objectives of the research have developed with time. They are: 1) to reemphasize the most suitable physiological applications of metabolic body size, 2) to relate the coefficient and exponent of that equation with fundamental force, and 3) specifically to encourage the students here to lay stress on the mathematical development of physiology and to relate mathematically their recommendations in applied animal husbandry to the total organism.

Theoretical Considerations

Entities in the environment that may cause important differences in the resting metabolism of animals are: gravity, air, light, temperature, water, food, and physical insults. These are arranged in order of stability—from gravity, which normally does

not change within the lifetime of most animals, to food, which may change with each meal, and physical insults such as toxins that may occur at any time in a random fashion. While gravity is a newcomer to this list its stabilizing effect on basal metabolism permits one to use an easily computed benchmark in defining the energy of basal metabolism (McMahon, 1973; Kleiber, 1969; Economos, 1979).

A brief review of the fundamental principles involved in relating animal form and processes to physical forces is in order. These have been reviewed by others (Schmidt-Nielsen, 1978; McMahon, 1973; Thompson, 1961; and Economos, 1979).

Brody (1945) noted that if one compares the general population of interspecies means with the intraspecies means, the intraspecies range may be short in dimension, such as obtained by Mrs. Bradfield on college girls over a narrow range in age. The exponent for surface area is only .55; in other words, form and specific gravity vary with size at constant age in a different manner than with changing age during growth. Brody also noted a similar exponent, .56, for resting metabolism of growing cattle between puberty and 30 months of age. Kleiber (1975) was explicit about the physiological conditions in which metabolic body size was a useful mathematical term. He states, ''Metabolic body size is applicable for expressing the interspecific mean for basal metabolism in mature animals of similar physiological status.'' He recognized, as did Brody, age and fatness were important factors in altering the resting metabolism of animals. Thus, one should not use this term outside of the general population of interspecific means or without attaching to it an appropriate term to describe the differences in physiological condition (Kleiber, 1975).

Economos introduced new terms for Kleiber's equation:

$$E_m = 70W^{3/4} \tag{1}$$

Where E_m = basal metabolic rate in kcal per day
and W = body weight in kg

He used systems analysis to approximate the expected terms from growth repression. He then used the rate of metabolism of glucose in the diaphragm and maximum growth repression coefficient of 11% per unit gravity to formulate a new equation:

$$E_m = 58W^{.67} + 12W^{.89} \tag{2}$$

In this equation he states that the term $W^{.67}$ is the variable representing loss of heat of the surface area and $W^{.89}$ is associated with gravity since it is computed as a standardized variable for growth repression (Economos, 1979). The variable for growth repression appears near expected values (Kleiber, 1969). In interpreting this two-compartment equation Economos seems to be saying that the egress of heat by way of the surface area is somehow differentiated from the heat production associated with gravity. There are deviations of his linear regression at the extremes resulting in a cool elephant and a hot mouse. He also introduces the questionable concept of mass at the earth's surface of less than one. There is need to further examine the particulars of the difference between the surface area exponent of the 2/3 power and the metabolic body size exponent of the 3/4 power.

Since Galileo (1638) we have known that the form and structure of animals change with increased size to meet the changing points of weight and the enormous load of animals, or those animals may break down under weight of growth. The changing structural form of animals has been most explicitly determined by

Heusner, described by Schmidt-Nielsen (1978) and Kayser and Heusner (1964). The regression of the skeleton weight on body weight in kilograms using the log scaling resulted in an exponent of 1.13. The changes in skeleton of animals are described:

$$\text{Skeleton Weight } (X_w) = k_x W^{1.13} \qquad [3]$$

$$\text{For Mammals } (X_w) = .085 W^{1.13} \qquad [4]$$

These measurements lead Schmidt-Nielsen (1978) to conclude, ''Weight of the skeleton of mammals increases more than proportionately to an increase in body weight since skeletons must be scaled to support the weight of the body as its bulk increases with the third power of the linear dimensions.''

The birth weight of cattle quadruples approximately twice during a lifetime. In addition, structural proteins and minerals compound continuously in amounts in relation to the increasing mass of the body. Quadrupling occurs from birth to puberty and again from puberty to maturity. Thus, if one corrects for the differences in body composition, mature weight may be computed by:

$$\text{Mature weight } (W_m) = k_{pn} W_b (4^2)^{9/8} \qquad [5]$$
$$\text{Where } k_{pn} = \text{postnatal dehydration} (1 - \% \, \Delta \, H_2O)$$
$$W_b = \text{birth weight}$$
$$4^2 = \text{inherent growth}$$
$$9/8 = \text{gravity-effected growth rate}$$

for Holstein cattle of 650 kg,
$$W_m = (.88) (41) (18)$$

Protein forms a constant proportion of the lean body mass, whereas the proportion of protein in the total body mass declines as body fat accumulates. Considering that the muscles attached to the skeleton, as the skeleton, are increasing more rapidly than the body, one concludes that other forms of protein must be diminishing concomitantly. Brody prepared an interspecies comparison of organ weight with increasing body weight among mammals and birds and showed that most organs and glands tend to decrease with increasing body weight. In particular he showed that liver weights increase only 87% as the body weight increases by 100%. Thus, the increase in skeleton and muscle weight is a mirror image of the decrease in liver weight as the body weight of mammals and birds increase. Similar results are noted for the kidney.

In considering muscle as an inherent source of heat production of basal metabolism, one needs to consider the net force of gravity on the muscle. If the animal is reclining, the principal effect of gravitational force is on the muscle and the attached bone. The first principles of buoyancy were introduced by Archimedes (287 to 212 B.C.). His principle states that a body immersed in a fluid is buoyed with a force equal to the weight of the fluid displaced. The correlate of this is that muscular response in resting animals is proportional to the density of muscle protein and its affixed bone minus the counterpoising buoyancy of tissue fluid in which it is bathed. Thus, it is the differential density of muscle that must be associated with basal metabolic heat production.

There are two other basic considerations pertinent to the mathematical calculations that follow. First, Tessier (1927) stated, ''Surface area varies with the square of linear size regardless of size provided only that the large and small animals are similar in the way that large and small circles are similar.'' For my calculations we included length of body and considered animals as a group of cylinders. It was Mellor (1915) who noted that ''if nature were our banker she would not add the

interest to the principal every year, rather the interest be added to capital continuously from moment to moment.'' I have consistently used $W^{9/8}$ as a compounding multiplicative term in computing the change in growth with increasing body weight.

Linear Dimensions and Lateral Growth

Table 1 presents the allometries of various dimensions in growth to note specifically the relative difference in lateral growth as indicated by the torso, $W^{3/8}$, and length and height, $W^{1/4}$. If one has proportionate growth in all dimensions, then the surface area is according to weight to the 2/3 power. However, if growth of a cylinder-like object is restricted to lateral growth, the proportionality to surface area is the 1/2 power (Table 2).

If one considers the increasing density of specific tissue during growth and its displacement of water under conditions of lateral growth, the proportionality is computed to be to the .56 power. This is the same as observed for cattle by Brody (1945) and for sheep by Ritzman and Benedict (1931). These results are in line with the observation by Brody that growth is proportionately larger in those dimensions that measure the torso of cattle than in those that measure the height or length. After puberty, changes in the surface area, frame size, and the accumulation of muscle is more nearly in accord with lateral growth since long bone growth is diminished. Changes in surface area measured by the law of regression therefore would reflect changes according to 1/2 power of the body weight compounded for inherent effects of gravity on growth, $W^{.5625}$.

The results on linear dimensions of dairy cows in which the width is measured at the tuber coxae are presented in Table 3. These results are commensurate with torso allometry and a compounding effect associated with the changing form of animals carrying increased weight; that is, their skeletons increase at the 9/8 power over the mean linear dimension $W^{.333}$ and is the theoretical difference between the surface area measurement of weight to the 2/3 power and the metabolic body size weight to the 3/4 power. Skeletal growth was evaluated as a factor in metabolic size. It was known already that the skeleton of animals increases with the increasing body weight, weight to the $W^{1.13}$. Similarly, in this experiment using data collected on 100 cows the change in the cube of the linear dimension width of the hooks was proportionate to $W^{1.12}$. Relating lateral growth of the skeleton to body mass with gravitational pull, one obtains the formula for surface area,

$$S_A = k_s(W^{1/2})^{1.12} \tag{6}$$

which resolves to:

$$S_A = k_s W^{.56} \tag{7}$$

This is the same as was found by Brody. The concomitant increases in metabolism accompanying the gravitationally modulated gain in skeleton width would be associated with a larger body surface area. For metabolism,

$$\text{Metabolism [M]} = k_m(W^{2/3})^{1.12} = k_m W^{.75} \tag{8}$$

which is the formula of Max Kleiber for metabolic size.

The linear dimensions for calves are in Table 4. The result shows that torso growth of calves is proportionately double that of growth in cattle after puberty, suggesting that the change in surface area with total body weight is increasing twice

Table 1. Body Weight Relationships, Any Shape, At Constant Density[1]

$W^{1/3}$ = proportional to a linear measurement

$W^{2/3}$ = proportional to surface (S_A) in three dimensional growth

$W^{3/8}$ = proportional to linear dimensions of torso

$W^{1/4}$ = proportional to length

S_A = $kW^{2/3}$ = $10W^{2/3}$ for animals

$kW^{1/2}$ = proportional to surface area in lateral growth only

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[1]Brody, 1945, and McMahon, 1973.

Table 2. Lateral Growth and Surface Expansion

	Exponent, Sa
Cylinder (Constant Density)	.500
Cylinder (H_2O → Bone[1])	.568
Cattle (Brody, n = 96)	.560
Sheep (Ritzman and Benedict)	.561

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[1]Bone mineral was judged to be 32% of the skeleton.

Table 3. Tuber Coxae (Hook to Hook) Width and Body
         Weight in 50 Holstein and 50 Jersey Cows

Time	Intercept	Slope	Equation[1]
Two months in lactation	.7207	.372	$5.25\ W^{.372}$
Ten months in lactation	.7243	.368	$5.30\ W^{.368}$

[1]Coxae width is in centimeters and body weight (W)
 in kilograms.

Table 4. Allometric Equations for
          Height, Length, and Width of
          Calves Where W = Weight

Height = $32.5\ W^{.22}$ (r^2 = .861) n = 100

Length = $20.8\ W^{.284}$ (r^2 = .857) n = 100

Coxae = $3.57\ W^{.414}$ (r^2 = .961) n = 52

as rapidly in lateral dimension. This lead to the hypothesis that the heat loss of young animals associated with the rapid growth in muscular and bone development and measured by the 9/8 power in cows would be a 10/8 power in young calves.

Energy Metabolism

Thus far we have discussed growth and the partition of growth in relation to dimensional analysis, its probable inherent relationship to gravity, and how these changes in the allometries of growth affect the log log plot of energy metabolism on total body weight. The pertinent information with regard to the relationship of gravity to metabolic body size and its coefficients comes from energy metabolism trials. The logarithms of resting metabolism of 30 calves were regressed on the logarithms of the body weight giving:

$$\text{Metabolism (M)} = 96.8W^{.8121} \qquad [9]$$

Brody had obtained for Holstein calves:

$$M = 88.3W^{.84} \qquad [10]$$

and for Jerseys:

$$93.0W^{.81} \qquad [11]$$

Analysis of the residual errors from equation [9] showed that most of the values were in the first and third quadrant. It was suspected that an association could be made with exponential growth. A multiple regression of $\log_{10}$ of resting metabolism (M) on the rate of change ($\Delta W/t$) and $\log_{10}$ body weight (W) was done. The model, equation [12]:

$$M = AW^b \cdot e^{k\Delta w/t} \qquad [12]$$

The exponential equations resulting from the statistical analysis and summation of the data are:

$$M = 118\ W^{.743} \cdot e^{.18\ \times\ 10-3\ \text{g/d}} \qquad [13]$$

$$M = 118\ W^{.743} \cdot e^{.18\ \text{kg/d}} \qquad [14]$$

It is noteworthy that the exponent of the body weight was now .743 which could not be considered different from .75. The conclusion is that the resting metabolism of calves is the summation of the heat production associated with the normal metabolism of muscles and the effect of their supporting structures and a porportionate growth constant $e^{.18}$, a variable for the daily gains in kilograms per day. The coefficient, .18 of equation [14], was of special interest since it did not differ from the standardized variable, the reciprocal of the turnover time used in determining metabolic age (Taylor, 1965). In view of the fact that a similar result was obtained when the metabolic time was calculated for the metabolism in rats described by Kleiber et al. (1956), the model for equation [12] becomes:

$$M = AW^b \cdot e^{k\Delta W/t} \qquad [15]$$

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Thus the constant for the multiplicative function for growth from basal metabolism was the reciprocal of the metabolic turnover time in the equation for basal energy needs for growth in calves. The general result is in equation [16]:

$$M = 116\ W^{.75}\ e^{kg/dW.27} \qquad [16]$$

$$\text{where, } M = \text{basal metabolism}$$
$$W^{.75} = \text{metabolic body size}$$
$$K = 1/t_t = 1/W^{.27} \text{ and } W \text{ is mature wt}$$
$$\Delta W = \text{kg, daily gain}$$
$$t = \text{day}$$

The constancy for basal metabolism is not only the result of the constancy of $W^{.75}$ as an interspecies mean but the constant itself, approximately 70, appears the same for a large group of animals when compared across species. However, since the constant decreased from 118 in calves of different breeds at birth to 70.5 in mature animals of similar physiological condition it was considered that the constant for different physiological conditions is set by the different amounts of protein in the body. It was reasoned that the stable force for heat production that is associated with the proteins was measured by that proportion of the protein represented by its density above the density of physiological fluid.

The relevant factor is the buoyant force of extracellular foods and Archimedes' principle applies. If one multiplies a partial density of the structural proteins and bone by the force of gravity at the earth's surface and the other needed constants, one should obtain a result comparable to the constants 70.5 and 118. The model for these computations is in equation [17]:

$$M_{kcal} = g \cdot W \cdot \Delta H \cdot t \cdot (\Delta d_p \cdot P + \Delta d_b \cdot B) \qquad [17]$$

$$\text{where, } M = \text{resting metabolism}$$
$$g = \text{gravity}$$
$$W = \text{weight}$$
$$\Delta H = \text{calories per newton-second (M kg sec)}$$
$$t = \text{time}$$
$$\Delta d = \text{proportion of density greater than body fluid}$$
$$P = \text{protein in body muscle}$$
$$B = \text{bone in body}$$

The pertinent computations are in Tables 5 and 6. The results of those computations show that the most important probable role of gravity on metabolic body size in homeotherms is stabilization of heat production resident in the muscle attached to the skeleton. The interpretation of this result may be different depending on where one's scientific biases lie. We might say that in competitive survival among homeotherms the surviving animals are those with weights and contents of structural parts most nearly proportionate to the force of gravity, or that gravity is the set force for the basal metabolic heat resident in the muscles of homeotherms.

The application of these results is convincing (Figure 1). The comparison of 12 metabolism trials with calves 51 kilograms in weight and mature Holstein cows, nonlactating, of 622 kilograms in weight show that the slope of the resting energy metabolism from calves to cows was .56. After adjusting the values for growth using equation [16] and its counterpart for mature cattle, the slope was .67, similar to a value for surface area. We interpret this to mean that the structural protein of cattle and their surface areas are highly correlated. This is commensurate with the hypothesis that lateral growth of bone and muscle is continuous with weight gain.

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Table 5. Computation of Coefficient of $70 \, W^{3/4}$ in Mature Cows

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$g = 9.8 \text{ ms}^{-2}$ $\qquad\qquad\qquad\qquad$ $W = 1$

$\Delta H = 2.34 \text{ cal newton-second}^{-1}$

$t = 86{,}400 \text{ sec.} \cdot d^{-1}$

$\Delta d_p = \dfrac{1.316 - 1006}{1.316} = .236$

$P = .0943$ (body protein $= 15.1\%$)

$\Delta d_b = \dfrac{3.115 - 1.006}{3.115} = .677$

$B = .0197$

$9.8 \cdot 1 \cdot 2.34 \cdot 86{,}400 \cdot (.236 \cdot .0943 + .677 \cdot .0197)$
$= 70.5 \text{ kcal/d}$

Table 6. Computation of Coefficient for Resting Metabolism at Birth

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$g = 9.8 \text{ ms}^{-2}$ $\qquad\qquad\qquad$ $W = 1$

$\Delta H = 2.34 \text{ cal newton-sec.}^{-1}$

$t = 86{,}400 \text{ sec.} \cdot d^{-1}$

$\Delta d_p = .236$

$P = .198$

$\Delta d_b = .677$

$B = .0177$

$9.8 \cdot 1 \cdot 2.34 \cdot 86{,}400 \cdot (.236 \cdot .198 + .677 \cdot .0177)$
$= \underline{116.3} \text{ kcal/d}$

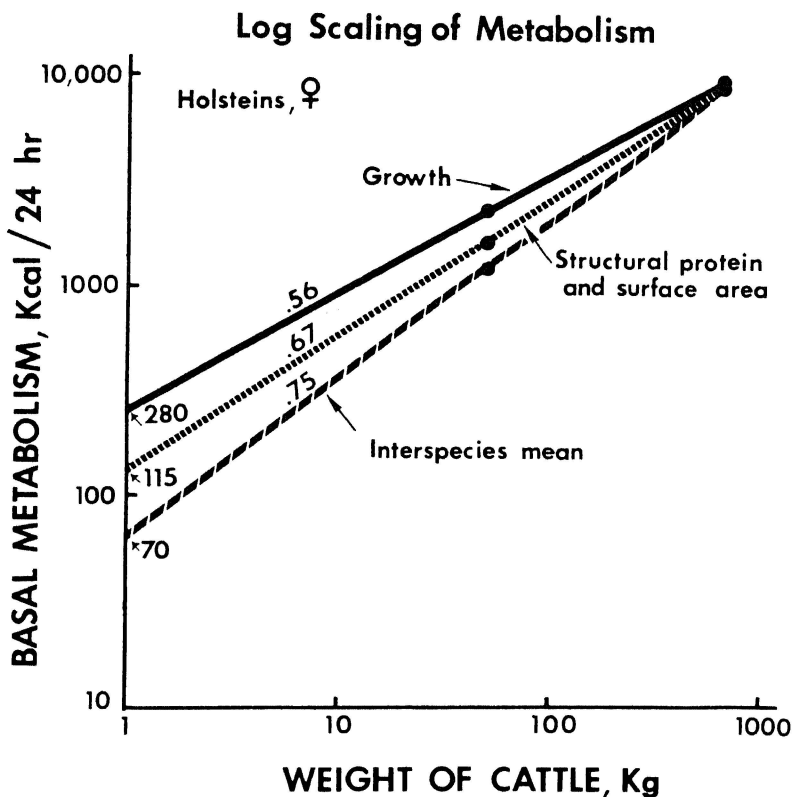Empirical $M = \underline{118} \, W^{.814} \text{kcal/d}$

Figure 1. The basal metabolism of cattle adjusted for differences in growth and body composition. Solid line (━━━) observed results with 12 trials with three calves and 12 trials with three nonlactating cows, cross-hatched line (••••••••••) after the energy metabolism of all cattle were adjusted for energy requirement for weight gain, and slant-hatched line (◢◢◢◢) after a stepwise proportional adjustment of energy metabolism with body-protein ratios to level of mature cattle.

Finally, a further adjustment of the calf structural protein to the same percentage as mature cattle and a concomitant decrease in energy results in a slope of .75 with an intercept of 70. The conclusion is that the difference in structural protein and the net energy associated with growth cause calves to differ from cows in their basal metabolic rate.

Summary and Conclusions

Basal metabolism in homeotherms is closely aligned with force of gravity. The change in amounts of structural protein and bone associated with increasing size among species results in a 12½% increase in the ratio of metabolism to weight above the computable surface area. This is an increase of 8.33% in energy metabolism with each 100% increase in weight and is precisely correlated with differences in lateral growth from the mean linear dimension $W^{.333}$. The stability of basal metabolism arises from its constant relationship to gravity mediated by heat production in muscle and the use of muscle to support the body mass. Most of the important variations in basal metabolism were ascribable to net energy for support of growth and differences in protein content of the body. In this view the energetic cost of organs such as the liver is low during postabsorptive state and is properly a component of the heat increment.

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