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Metabolic Rate and Food Utilization as a Function of Body Size

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BRODY MEMORIAL LECTURE I

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METABOLIC RATE AND FOOD UTILIZATION AS A FUNCTION OF BODY SIZE

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BRODY MEMORIAL LECTURE I

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I. INTRODUCTION

I am grateful for the honor which you have bestowed upon me by inviting me to give the first annual Brody Memorial Lecture. I owe to Samuel Brody the opportunity to give my first lecture in America which was also my first Sigma Xi lecture. That was in May 1929, on this campus. The lecture dealt with the energy concept in Animal Nutrition, the content of my inaugural lecture as Privat Docent at the Swiss Federal Institute of Technology at Zurich. I remember that I discussed the guiltiness of the second law of thermodynamics. I have learned since that the proper translation of the German "Gültigkeit" is validity rather than guiltiness.

When our hair turns white and our dignity becomes official by the title Emeritus we love to reminisce - and I know of no better opportunity to indulge in this habit and, indeed, justify it, than a Memorial Lecture. So I am going to tell you something of the cooperation between Samuel Brody and myself and to show that the work of one supplemented in a way that of the other.

In Wilhelm Ostwald's classification, Samuel Brody was a romantic scientist, as Liebig had been. He had a wide range of interests, was full of ideas, and had the energy to put these ideas to work. He had the ability to induce his enthusiasm into others and fortunately, into people who control research funds. He was an inspiring leader of research, and he and his co-workers produced an amazing amount of data. Brody had the tenacity to keep on working until his results were published in bulletins and in his book, which can be used as an encyclopedia of animal energetics.

Where do I come in? Don't worry, I won't keep that little light of mine under a bushel. Brody was the great producer of results. His main contribution was induction; my speciality in our cooperative effort was testing generalizations by deduction. This testing sometimes led to the rejection of proposed hypotheses. Emil DuBois congratulated me

once for the debunking job done in my review "Body Size and Metabolic Rate" (1947). But I also indulged in formulating generalizations, and Brody found them useful, providing pegs on which to hook ideas.

I hope that this memorial lecture will provide an example for the sound rule that respect, and even strong personal affection, for a colleague - as I always felt for Sam Brody and still feel for H. H. Mitchell - does not prevent a scientist from openly and strongly expressing differences of opinion. The competition of ideas is essential for progress in science, and this competition, you may call it fight if you like, should not be inhibited by friendship and, in turn, should not diminish friendship.

II. BODY SIZE AND METABOLIC RATE

A. Origin of the Surface Law

In 1839, Dr. Sarrus, a professor of mathematics at Strasbourgh, and a scientifically minded physician, Dr. Rameaux, living in the same city, sent to the Royal Academy of France a paper in which they speculated that Nature never used one means of achieving her purposes but let two means compete. The metabolic rate of animals might possibly be independent of body size, or it could be proportional to body weight, or the cube of a linear dimension. Nature chose some relation between these extremes and made the metabolic rate, and also the rate of blood flow, proportional to the square of a linear dimension.

That was the beginning of the Surface Law of metabolic rate.

This law was later discovered "après coup", that is empirically, by Richet who measured the metabolic rate of rabbits, and by Rubner who observed the metabolic rate of large and small dogs and later concluded that all homeotherms produce daily 1000 kcal of heat per square meter of body surface.

B. Surface Area

1. Approximations. To Sarrus and Rameaux, surface meant just the square of a length. Richet preferred a more concrete concept. He calculated the surface areas of his rabbits from their weights, assuming the rabbits were spheres with a density of 1.

The surface of a sphere can be calculated from the volume by the equation:

$$S = 4.84 \times V^{2/3}$$

where S = Surface area in dm^2

V= Volume in liters

with density = 1, V = Weight in kg.

2. Search for "true surface". Meeh decided that the animals were really not spheres and formulated the surface area of animals as follows:

$$S = k \times W^{2/3}$$

where S = Surface area in dm^2
W = Body weight in kg.

The Meeh constant is the relative surface area of animals $S/W^{2/3}$. It is the same for animals of similar build. It is greater the more the shape of an animal deviates from that of a sphere.

For several decades the measurement of animal surface areas was in fashion in many physiological laboratories. Ingenious methods for such measurements were invented, such as skinning the animals, or adjusting a mold and then flattening it out for measurement. Rubner covered the body of men and women with tin foil and weighed the amount of tin foil used for that tapestry job.

Such measurements were undoubtedly enjoyable but time consuming, and some of these animal and human surveyors felt that their fellow physiologists could save time by calculating instead of measuring surface areas. They expressed, therefore, the results of their measurements as Meeh constants. Instead of covering the body of a girl with tin foil the physiologist had only to look up a Meeh constant and multiply it with the 2/3 power of body weight. That saved time and was less exciting.

But one could question whether or not the Meeh formula was really adequate to express the "true" body surface. Which of the various Meeh constants for human beings, for example, should one use? You had to judge the degree of deviation from a spherical shape. This deviation increases with the degree of slenderness.

To take care of this situation, DuBois and DuBois (1916) developed a formula for calculating the surface area of men and women from weight and height as follows:

$$S = 71.84\ W^{0.425} \times L^{0.725}$$

where S = Surface area in cm^2
W = Body weight in kg
L = Body length in cm

since W is proportional to the cube of a linear dimension, $W^{0.425} = k\ L^{1.275}$ and therefore $W^{0.425} \times L^{0.725} = k\ L^{1.275} \times 0.725 = kxL^{2.000} = kxW^{2/3}$ the formula is therefore dimensionally correct. It expresses surface area as the square of a linear dimension or the 2/3 power of Volume.

A nomogram for surface vs. height and weight of man has been published recently by J. Sendroy and H. A. Collison (1960). They use a dimensionally incorrect formula.

A dimensionally correct formula will give a correct answer not only for a given set of measurements but generally, also, when applied to large and small bodies of similar shape. The coefficient, for example the Meeh constant, or the factor 71.84 in DuBois formula, is a term without dimension.

3. Irrational power of Weight. As Meeh had replaced Richet's

sphere constant, 4.84, by multiplying the 2/3 power of weight by a variable k, so later physiologists replaced Meeh's constant exponent of the body weight (2/3) by a variable exponent p.

They formulated

$$S = k \times W^p$$

Brody was among those physiologists. He operated a surface integrator roller which can be used like that with which a printer puts printer's ink on a plate. This apparatus is rolled over the surface of animals. The number of times required for the complete paint job (if the roller had actually been depressed in print) indicated by a revolution counter is then multiplied by the lateral surface area of the cylinder. The product is the surface area of the animal.

Brody, et al (1928) measured the surface area of 482 dairy cattle, 341 beef cattle, 11 horses and 16 swine.

Brody then plotted the log of the surface area against the log of body weight. A straight line resulted. This indicates that

$$\frac{dA}{A} = k \frac{dW}{W}$$

the relative change in area is proportional to the relative change in weight and that

$$A = c\ W^p$$

the area is proportional to a power function of the weight. He discusses various complicating expressions but states (p. 12)

> this substantiates the idea that in the vast majority of cases the simple equation involving weight only as a datum on the right side of the equation suffices to represent the relation between surface area and body size in domestic animals.

Brody, et al. (1928) conclude (p. 37) that the application of the practice of relating heat production to surface area

> . . . . may be justified by custom, it is entirely unnecessary in principle. They write later, it is simpler to relate heat production to a power function of body weight. . . . than to relate heat production to surface area.

4. Mitchell's criticism (1930), p. 444,445, of Brody's simplification* stimulated my own interest in this area of research. In an article devoted to the significance of surface area determinations, Mitchell (1930) reports the results of his measurements of rat surfaces, a job considerably easier than the measurement of human surfaces be-

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* See Page 9.

cause it is not against the law to skin rats. The major results of these measurements are shown in Slide 1.*

A rat weighed 413 grams, the area of the skinned carcass, measured by a mold, amounted to 430 cm^2, the unstretched skin had an area of 536 cm^2, and a moderate degree of stretching brought this to 630 cm^2.

The area, calculated by the ordinary Meeh formula with a Meeh constant of 10, is 556 cm^2.

What is the "true" rat surface? Mitchell concludes as follows:

> With chickens and rats, and presumably with other animals also, the surface area is not a definite measurement.

But, after having thus clearly stated that surface area cannot be properly defined, much less definitely measured, Mitchell concludes his lucid article with the rather obscure statement:

> Needless to say, the method of eliminating the effect of differences in size of the animal upon basal heat production by expressing the latter per unit body area is just as valid as ever.

The surface area is not properly definable but its application is valid. A psychological explanation for this strange contradiction may be found in Mitchell's subsequent article (1930) where he writes as follows:

> In undertaking the determination of the surface area of a considerable number of animals by an exacting and time consuming method, and in burdening the literature with a description of the results secured, one should have a definite conviction of the value and significance of surface area and determinations.

The argument seems to be as follows: Since we have measured the surface of many animals by time consuming methods, since we have burdened the literature with the results of such measurements, we have to stick to the conviction that these measurements were significant and valuable despite our recognition that surface area cannot be properly defined or definitely measured.

To demonstrate his conviction that the determination of animal surface area is worthwhile, Mitchell measured the surface area of chickens.

From his measurements he derived the following regression equation:

$$S = 8.19 \times W^{0.705}$$

where S is the surface area in cm^2
and W is the body weight in grams

he states that this formula is a distinct improvement over the Meeh

*Slides included in Appendix, page 30.

formula which would summarize the same measurements as follows;

$$S = 10.64\ W^{2/3}$$

The average percentage deviation between predicted and observed surface area (irrespective of positive or negative sign of the deviations) amounted to 5.61% when the Meeh formula was used and to 3.73% for Mitchell's prediction based on the 0.705 power of body weight. This small improvement of accuracy seems irrelevant especially if one consider Mitchell's own statement that surface area is not a definite measurement.

What does one percent greater accuracy mean when in the definition of the surface area 10 or even 20% of the area is doubtful? The question has, for example, been raised whether or not the surface area of the rabbit ears should be added to the rest of the rabbit surface. This means an uncertainty of 20%.

The Meeh calculation based on the 2/3 power of body weight is theoretically preferable to Mitchell's calculation with the 0.705 power because Meeh's formula expresses surface area in a rational dimension, the 2/3 power of a volume.

Animal growth is ordinarly allometric, and the allometric growth of surface area in a growing animal is expressed by a weight exponent which differs from 2/3. Mitchell's formula for chicken surface $S = 8.19\ W^{0.705}$ indicates that the surface area grows faster than in proportion to the 2/3 power of weight. The relative surface area, $S/W^{2/3}$, of older chickens is larger than that of younger chickens. This behavior can be brought out more clearly by expressing surface area as a product of the isometric size effect (the Meeh formula) and a factor for allometry.** This is shown in Slide 2.

The factor for allometry ranges from 0.916 to 1.028 as the chicken grows from 100 g to 2 kg of weight. Instead of relating allometry to body weight, it might be preferable to relate it to age by the equation:

$$S = \left[10.6 \pm s\,(A - \bar{A})\right]\ W^{2/3}$$

Where A = age, $\bar{A}$ = mean age

s would then express the effect of age on the shape of the animal expressed as relative surface area (Meeh constant).

Over the entire range of Mitchell's chickens this age effect amounts to only 11% of the relative surface area (0.916 to 1.028). Considering the vagueness of the definition of animal surface the significance of the allometric age effect on surface area is questionable. (This is especially true for the application of surface area to animal heat pro-

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**We can write $S = 8.19\ W^{0.705} = 10.6\ W^{0.667} \times a\ W^{0.038}$

for $W = 1$, $S = 8.19 = 10.6 \times a$

therefore $a = 8.19/10.6 = 0.77$

duction.)

5. Confusion by "true" Surface. Quite generally, the search for a "true" animal surface has proved futile and it has even become more of a hindrance than a help in the understanding of metabolic rate. This is shown in Slide 3. (Rat Surfaces in 1943).

I am sure you will understand the frustration of a reviewer who attempts to compare the results of the various laboratories on rat metabolism, and you will agree with the suggestion that (Kleiber, 1944), "the time is ripe for asking authors who use their personal rat surfaces, to supplement their figures with data which make their results comparable with those of other workers. Metabolic rate per animal together with the weight should at least be given."

C. Theoretical Validity of Surface Law

1. Physical significance of surface law. Brody (1928) concluded that metabolic rate could just as well be related to a power function of body weight than to surface area. Mitchell (1930), however, maintained that

> the relation between surface area and basal heat out put possesses a physical significance which is entirely ignored in Brody's recommendation that the basal metabolism be considered merely as a power function of body weight rather than as a function of body surface.

The major reason why Brody, and earlier Krogh (1916), suggested a power function of body weight instead of surface area is that the latter is ill defined, as we have just discussed. But let us forget, for the sake of argument, the poor definition of surface area and investigate the validity of the theory that the metabolic rate is proportional to the surface area.

We can distinguish 5 types of explanations for the surface law:

(1) The heat loss is proportional to surface area.
(2) The rate of blood supply to the tissues is proportional to the surface area.
(3) The diffusion area to the interior of the cells is proportional to the surface area.
(4) The weight of metabolically active organs is proportional to the surface area.
(5) The amount of active protoplasma is proportional to the surface area.

2. Three invalid theories. Let us first discard the 3 last explanations and then discuss how valid the first and second are. The amount of active protoplasm is measured by the metabolic rate, therefore the metabolic rate is proportional to the amount of active protoplasma. Any objections? This is known as a tautology. It is the only

one among the 5 explanations which is absolutely correct and explains absolutely nothing.

The cell surface theory can be dispatched quickly. True, all the oxygen and all the nutrients which are involved in the metabolism in the cells have to diffuse through the cell surfaces, but the sum of these surfaces is not proportional to the body surface area. This proportionality could only exist if the cell size were in proportion to body size. If a human cell weighed, say, on the average, 1000 times as much as a rat cell, or were 10 times as long as a rat cell. One might construct such animals with isometric cells for a book on science fiction. In nature they do not exist. Larger animals have more cells than smaller animals, rather than bigger cells.

The explanation based on organ weight needs more discussion. Brody et al. (1928) wrote as follows,

> The weight of the kidney, the weight of the liver and practically the weight of the lung, blood, stomach and intestines increase directly with the body weight at the same relative rate as does the surface.

I do not doubt the correctness of Brody's measurements, but I reject their generalization, especially as an explanation for the surface law. Here is where deduction plays a useful role. That, as said above, was my specialty in the team work with Brody. If it were generally true that blood volume is proportional to surface area, or to the 2/3 power of body weight, then one could calculate the blood volume of a 70 g rat from that of a 70 kg man.

This calculation and its bloody result are shown on Slide 4, The Bloody Rat. Something is obviously wrong with the statement that the weight of the blood is proportional to the surface area. The error occurs very often in the literature. A result obtained from correct observations on a narrowly limited material is generalized and thereby becomes erroneous.

A good example is the old conclusion of Dryer and Ray (1910) that blood volume is proportional to body surface.

The results are shown in Slide 5, Blood volume and body weight.

Column 4 of Slide 5 clearly shows that the factor, by which $W^{2/3}$ is multiplied, increases systematically with increasing body size. This suggests that a closer relation would be obtained with a higher power of body weight than 2/3. Indeed, column 5 shows that blood volume per unit weight (rather than that per unit area) is independent of size, in contradiction to Dryer and Ray's generalization.

Similar deductions can be obtained from the theory that the weight of the liver is proportional to body surface, which furthermore would explain the surface law only if the liver of large and small animals

had the same metabolic rate per gram. Grafe (1925) and Terroine and Roche (1925) indeed reported observations indicating that the rate of oxygen consumption per unit weight of horse liver in vitro is the same as that of rat liver. However, later measurements in my own laboratory, indicated, to the contrary, that the metabolic rate in vitro shows the same effect of body size as the metabolic rate per unit weight of the animal. (Kleiber, M. 1941).

This relation is shown on Slide 6 - QO_2 of liver slices in vitro.

Krebs (1950) later confirmed these results with liver slices but found that kidney slices did not show a size effect.

The relative weight of the brain has been used as explanation for the surface law. Deductions based on this theory lead to similarly absurd results as was shown above for blood and could be shown for liver. Furthermore, women have almost exactly the same basal metabolic rate as sheep of the same body weight, but their brain weight is of a different order of magnitude. How then could brain size determine metabolic rate?

3. Two valid theories. Only two types of explanation for the surface law stand critique, namely, the heat loss theory and the theory connecting blood circulation with metabolic rate.

The heat loss of animals can be expressed as Fourier's law which makes the rate of heat flow through a surface layer of a warm body proportional to the surface area, and the ratio of the temperature difference across the surface layer and the resistance to heat flow.

$$\frac{dQ}{dt} = S \frac{T_i - T_s}{r}$$

Q = heat (calories)
S = surface area
T_i, T_s = Temperature of interior and surface
r = resistance to heat flow.

Since the resistance to heat flow can be changed by a process known as physical temperature regulation, a strict proportionality between rate of heat loss and surface area can not be expected.

That was shown in the classical experiments of Hoesslin with two dogs. A dog was raised in a warm climate, his litter mate in an ice box. The metabolic rate of the dog in the ice box was only 20% higher than that of his mild-climate brother. The ice box dog, however, had grown a fur which weighed three times as much as that of his brother.

The possibilities of changing the insulating power of the body covering are, however, limited. We can calculate that a mouse which produced only as much heat per unit weight as a steer, would need a fur of about 20 cm thickness to maintain its body temperature in a mildly cool environment. It is therefore understandable that a mouse with such a low rate of heat production per unit weight would have little

chance of survival. A steer with the rate of heat production per unit weight normal for a mouse, on the other hand, would have great difficulty to get rid of the heat fast enough to prevent overheating.

We can therefore understand that natural selection would produce large and small animals whose rate of heat production is approximately proportional to body surface rather than body weight. But we find no valid reason for the idea that the metabolic rate should be exactly proportional to a "true" surface rather than to the 2/3 power of body weight which latter is much better defined than the surface area.

We reach similar conclusions when we consider blood circulation. The pulse volume is approximately proportional to body weight. The frequency of heart beat, however, must be smaller for a horse than for a mouse for sheer mechanical reasons. A horse heart vibrating with the frequency of a mouse heart would hardly pump any blood.

Again this relation obviously does not permit the conclusion that the rate of blood flow and with it the metabolic rate of the animal must be exactly proportional to a definite surface area.

4. The biological explanation of the relation between body size and metabolic rate has been formulated as follows: (M. Kleiber, Hilgardia, 1932)

> In natural selection those animals are the most fit in which the caloric requirements for maintaining a constant body temperature are in harmony with the hemodynamic possibilities of oxygen transport.

D. Empirical Validity of Surface Law

We know now that the search for a "true" surface area of animals is futile. The best we can do is to define such an area in terms of a standardized measurement. We understand that homeotherms, which differ greatly in size, such as in rats and horses, could not get along if they had the same metabolic rate per unit weight. They would get into difficulty with heat exchange and also with circulation which transports oxygen and nutrients to the site of metabolism. We find, however, no support for a theory that the metabolic rate should be strictly proportional to a surface area resulting from even the most carefully standardized measurements. Now we can ask how accurately does the surface law represent the relation between body size and metabolic rate?

1. Surface law 1901 and 1931. European animals in 1901 obeyed the surface law very well indeed. This is shown in Slide 7. (The rabbit which was not too much of a conformist is left out).

I wanted to find out how much the surface law meant to American animals. Slide 7 shows the resulting rebellion of the American animals against the surface law in 1931. The slide also shows, however, that

there is not just a wild disobedience, but there is a well defined trend in the deviation from the surface law. The metabolic rate per unit surface area is higher the heavier the animal.

This consistent departure from the law encouraged the search for a formulation which would describe the relation of body size and metabolic rate more closely than does the surface law.

The surface area, as you remember, is proportional to the 2/3 power of body weight and if the metabolic rate followed the surface law it would also be proportional to the 2/3 power of body weight. The observation that the metabolic rate per unit of the 2/3 power of weight increases with increasing body size indicates that metabolic rate is more nearly proportional to a power of weight higher than the 2/3.

2. A weight power law. Applying the same method which Brody had used for calculating the relation of surface area and body weight, I plotted the logarithm of metabolic rate against the logarithm of body weight.

Slide 8 shows the result,

The equation for the linear regression without ruminants is as follows,

$$\log B = 1.872 + 0.726 \log W$$

If ruminants are included, the equation becomes:

$$\log B = 1.867 + 0.738 \log W$$

where B = metabolic rate in kcal per day

W = body weight in kg

1.867 is the logarithm of 73.7. We can therefore also formulate

$$\log B = \log 73.6 + 0.738 \log W$$

or

$$B = 73.6 \quad W^{0.738}$$

I was aware of the likelihood that with another set of data the power function may be different, but I felt justified to state (Hilgardia 6: p. 348, 1932):

> The results of recent work on metabolism of different animals from the ring dove and the rat to the steer shows a closer relation of the basal metabolism to the 3/4 power of body weight than to the geometric surface of the animal.

3. Brody's Confirmation. Soon after the publication of this result (Jan. 1932), I received a reprint of Brody's Research Bulletin 166, April 1932. Sam Brody wrote me personally, "Paper XXIII may interest you. I regret that most of it has been written after receiving your reprint".

Slide 9 shows the result of Brody and Proctor using a great variety of data on metabolic rates. The relation of metabolic rate and body weight summarized by Brody is

$$B = 70.4\ W^{0.734}$$

which is in amazingly close agreement with the summary in the Hilgardia article discussed above.

Brody and Proctor write (l.c.p. 101

> All one can say now is that the value of the true power lies between the limits of 0.64 and 0.72.

4. A "True Power" function? I do not think there is such a thing as "the true power". We can derive power functions which make predictions of basal metabolic rate more general, or more simple, than others do, and more accurate than surface area does, but the search for "the true power function" would lead into the realm of mystics where scientific inquiry is out of place.

At Brody's suggestion, the conference on energy metabolism held at State College, Pennsylvania in 1935, adopted (weight$^{0.73}$) as reference base for computing basal energy metabolism. I personally would have preferred a more rounded exponent, namely the 3/4 power. The question whether $W^{0.734}$ or $W^{3/4}$ fits the data on metabolic rate better would require a comparison between mice and whales.

Slide 10 (Ratio of weights required for establishing difference between W and $W^{2/3}$) shows that even the question whether metabolic rate is more nearly proportional to body weight itself, or to the 2/3 power of it, required a ratio of large to small animals of at least 2. This is concluded on the basis of the rather optimistic assumption that the prediction error is only $\pm$ 5% of the result. Generally one may formulate

$$p_1 (\log W - \log \overline{W}) - p_2 (\log W - \log \overline{W}) = \log (1 \pm 2\epsilon)$$

where W = body weight of heavy animal

$\overline{W}$ = mean body weight of population

p_1, p_2 = power of W to which metabolic rate is proportional

ϵ = error of estimate

For two straight lines on a log B, log W plot which cross at the log of the mean weight we may generally formulate:

$$\log B_1 = \log \overline{B} \pm p_1 (\log W - \log \overline{W}) \quad . \quad . \quad . \quad . \quad . 1)$$

$$\log B_2 = \log \overline{B} \pm p_2 (\log W - \log \overline{W})$$

Difference

$$\log \frac{B_1}{B_2} = (p_1 - p_2) \log \frac{W}{\overline{W}} \quad . \quad . \quad . \quad . \quad . \quad 2)$$

Where

B_1 = Metabolic rate predicted based on W^{p_1}

B_2 = Metabolic rate predicted based on W^{p_2}

$\overline{B}$ = Mean metabolic rate

W = Weight of large animals

$\overline{W}$ = Mean weight of large and small animals

p = Exponent of weight

from equation 2, it follows that

$$\log \frac{W}{\overline{W}} = \frac{1}{p_1 - p_2} \times \log \frac{B_1}{B_2} \quad \ldots \quad 3)$$

If the error of the estimate is ϵ % then the error of the difference between the two estimates is $\epsilon \times \sqrt{2} = 1.4\epsilon$. If we postulate that for significance the difference should be twice the error, then the difference becomes significant when it is 2.8ϵ. If ϵ be $\pm$ 10%, then for significance B_1 should be 28% greater than B_2 or the ratio B_1/B_2 should at least be 1.28.

With these figures eq. 2 becomes

$$\log \frac{W}{\overline{W}} = \frac{1}{p_1 - p_2} \log 1.28 \quad \ldots \quad 4)$$

if $p_1 = 0.75$ and $P_2 = 0.734$, $p_1 - p_2 = 0.016$,
the difference in estimate becomes significant when

$$\log \frac{W}{\overline{W}} = \frac{1}{0.016} \log 1.28 = 62.5 \times 0.107 = \underline{6.69}$$

$$\text{Therefore } \frac{W}{\overline{W}} = 4.9 \times 10^6$$

The ratio between the weights of the large and the small animals is twice the ratio between the weight of the large animals and the mean, therefore

$$\frac{W_{large}}{W_{small}} = 2 \times 4.9 \times 10^6, \text{ approx. } 10^7$$

To show a significant difference in the prediction based on $W^{0.734}$ and $W^{3/4}$, the large animals should weigh 10 million times as much as the small animals. We should compare mice weighing 10 grams with super mammals weighing 100 tons. No land animal reaches, or has ever reached, that weight. Only blue wales are reported to grow to 63 tons, one estimate of a sulphur bottom (Balaenoptera Sulfurea, Cope) is 147 tons (Heck, 1915).

5. Later confirmation of weight power law. In 1938, F. G. Benedict published the tremendous amount of information on basal metabolism collected by the Carnegie Nutrition laboratory in a book which has the rather queer title "Vital Energetics". On page 171, Benedict entered the basal metabolic rate of many groups of homeotherms from mice to elephants against body weight on a log-log plot.

Slide 11 shows this figure from which we can calculate that

$$\frac{\Delta \text{ log metabolic rate}}{\Delta \text{ log body weight}} \text{ is } 0.75$$

This is an excellent confirmation of our earlier results.

When, 9 years later, I was asked to review the topic of body size and metabolic rate for the Physiological Reviews (Physiol. Rev. 27, 530 (1947)), I collected data which had not been used before, cer-

tainly not in my Hilgardia article. The result of this new investigation again confirms the earlier conclusions.

Slide 12 shows Log metabolic rate/log body weight (Physiol. Reviews 27: 530 1947).

The best fitting power function of Weight this time is 0.756

The result could be summarized as follows:

$$B = 68 \times W^{0.756}$$

The mean error of prediction is $\pm$ 11% (antilog of 0.05) and with this error in mind the simpler equation

$$B_{(d)} = 70 \times W^{3/4}$$ for the daily metabolic rate

or $$P_{(h)} = 3 \times W^{3/4}$$ for the hourly metabolic rate for homeotherms with the body weight W in kilograms, was regarded as expressing best the law of body size and basal metabolic rate.

E. Intraspecific Prediction Equations

1. No need for general formulation? Keys and Brozek (1953) wrote in their review on body fat in adult man:

> Popular belief in the superiority of the body surface as the unit of reference is scarcely justified. If allowance is made for the inert mass of the body then the need for considering surface area or some similar complexity disappears.

and I answered to that (Kleiber, M. 1956):

> If a mouse physiologist or a rat-, or a man-, or a cow-physiologist is each interested only in the metabolic rate of his own special object of study then each can express the metabolic rate as a linear function of body weight $B = a \pm b \times W$. . . . . ."

2. But what does such an equation mean? It means that a man without weight produces a calories of heat and adds to that b calories for each kg of body weight. One may argue of course that man's weight stays within a certain range and we don't have to worry about a weightless man. One may accept this but soon the specialists will find that for species with considerable difference in size, such as dogs, different prediction equations have to be formulated for large and small animals of the same species. If the specialists had worked out all those linear equations, then some biologist who looks beyond one species may collect all these equations and compare them and he will find that similar equations fit small dogs, rabbits and chickens. He would discover that the equations for large dogs are similar to those for small sheep. He would conclude that differences in body weight affect metabolic rate more than differences in species and then, if he has some inclination for mathematics, he is going to find a formulation for metabolic rate which

is more meaningful than a multitude of linear regression equations. He would do what a geometer would do if he were to investigate the relation between the surface area and the volume of spheres)Kleiber 1950).

Slide 13 (Surface area and Volume of Spheres) explains this hypothetical procedure.

The surface area of spheres of different size is plotted against volume. In the region A of volume from 20 to 40, the surface area may be expressed as a linear regression equation (obtained perhaps by the method of least squares) as follows:

$$S = 15.1 \neq 1.04\ V$$

where S = Surface area
V = Volume

That a sphere without volume should have a surface area of 15.1 is somewhat disturbing, so we may try to investigate this by measuring surface areas of spheres in the region B with the result that

$$S = 3.14 \neq 2.28\ V$$

Now the sphere without volume has a surface area of 3.14.

It is also disturbing to note that the coefficient of weight differs. We suspect now that the surface area is not proportional to volume itself, but to a power function of volume different from 1. So we plot the log of surface area against the log of weight and find that both sets of our measurements now lie on the same straight line whose equation is

$$\log S = 0.684 \neq 0.67 \log V$$

and we derive from this linear logarithmic equation the relation

$$S = 4.84\ V^{2/3}$$

Now this makes sense: when the Volume reaches zero, the surface also disappears, and both sets of observations can be expressed by the same equation.

3. Intra specific application of weight power law. We have no a priori reason (like we have with spheresurfaces) to expect that we can express the metabolic rate of homeotherms with different body weights as a general function of this weight, but we have seen that, in fact, we can get good approximations by formulating

$$B = 70\ W^{3/4}$$

where B = daily metabolic rate in kilocalories
W = body weight in kilograms

Now we can postulate that this relation holds also within a species where the difference of size is usually too small to demonstrate it, because influences, other than size, become more important the smaller the differences in size. The change in shape may have an effect; age may have an effect. We can show this in the formulation of human basal metabolism.

In an attempt to avoid preconceived ideas like the surface law, Harris and Benedict (1919) expressed the relation of metabolic rate, body weight, stature, and age of men and women by empirical linear

regression equations. The claim that no preconceived idea is involved is erroneous. The calculation implies the postulate that the metabolic rate is the sum of a constant, a term proportional to body weight, another proportional to body length, and another proportional to age.

The result of this calculation is shown in the following equations:

For men $B = 66.4730 + 13.7516\ W + 5.0033\ L - 6.77\ a$ *

For women $B = 655.0955 + 0.6734\ W + 1.8496\ L - 4.6756\ a$

Where B = heat production in kcal per day
W = body weight in kg
L = length in cm
a = age in years

Some of the implications of these equations are obviously unsatisfactory, especially the idea that a woman without weight, age, or length has a definite metabolic rate which is 10 times that of a man having no weight, length, and age. Also the addition of non-additive items like weight, length, and age is not satisfying (add kilograms, centimeters and years.)

If we assume that the metabolic rate of men and women follows the same relation to body weight as that found by interspecific comparison, then we can use the measurements of Harris and Benedict (1919) and formulate the relation of human metabolic rate to weight, stature and age as follows:

$$B_{(men)} = 71 \times W^{3/4}\left[1 + 0.004\ (30-a) + 0.01\ (s - 43.4)\right] *$$

$$B_{(women)} = 66 \times W^{3/4}\left[1 + 0.004\ (30-a) + 0.018(s - 42.1)\right]$$

Where the symbols have the same meaning as above and s stands for

$$\text{specific stature} = \frac{\text{height in cm}}{W^{1/3}}$$

The terms of these last two equations have a rational physiological meaning. For men of the standard age of 30 years and the mean specific stature of men (43.4 $cm/kg^{1/3}$), the metabolic rate is $71 \times W^{3/4}$ or about 7% higher than the metabolic rate of 30 year old women of a standard specific stature of 42.1. Age has the same effect on the metabolic rate of men and women, 0.4% change per year, but the metabolic rate of women is more sensitive to changes of specific stature.

III. BODY SIZE AND FOOD UTILIZATION

The teamwork between Brody and myself is especially noticeable in the answer to the question how body size affects the efficiency of feed utilization. Brody was delivering the data while I did most of the theoretical speculation, furnishing, as Brody puts it †, the pegs on

* These equations were shown on Slide 14 in lecture

†Brody, S., Bioenergetics and growth, p. 49: "Generalizations of the type of Rubner's and Kleiber's necessarily involve large margins of error. Nonetheless they are useful serving as pegs on which to anchor ideas however insecurely."

which to hang the ideas.

A. Rabbit vs. Steer. I started my work on respiratory exchange and energy metabolism at Zurich with a rabbit as an inexpensive way of learning the tricks of the trade in this field of research. During that work I became curious to know how a rabbit would compare with a steer as a food utilizer.

Slide 15 shows that the rabbit utilized the metabolizable food energy in maize for the production of body fat, just as efficiently as (according to Kellner's investigations) a steer would have done. I mentioned this in a popular article (Kleiber, M. 1926). The situation, however, was not quite clear to me. To reach a better understanding of the relation of body size and efficiency of feed utilization I needed a clear definition of efficiency.

B. Two types of efficiency. We may distinguish two types of efficiency-total and partial efficiency.

1. Total efficiency. The total efficiency is the ratio of the total gain to the total food consumed

$$e_{tot} = \frac{G}{I}$$

Where G = gain
I = food intake

Gain and food intake may be expressed as weight, as kg dry matter or as energy.

We could, of course, express gain in energy of body substance per ton of food consumed or pounds of gain per megacalorie of digestible feed energy, but it is advantageous to express gain and food in the same units, pounds of gain per pound of food consumed or megacalories of gain per megacalorie of food consumed. In this case, the efficiency should be a term without dimension, usually expressed as a percentage, lbs. gained per 100 lbs. of food consumed, or megacalories of body fat or milk or work gained per 100 megacalories of digestible food energy, for example.

When Brody was working on a review on nutrition for the Annual Review of Biochemistry (1935), he wrote me if I had done anything on energy metabolism which he might include in his review. I sent him a copy of a manuscript "Body Size and Efficiency of Food Utilization" which I had sent to the Journal of Nutrition. Brody discussed this paper in his review and that remained the only place where it was published. The Journal of Nutrition in 1934-35 was overcrowded with manuscripts and had to give preference to papers which presented more original data than mine. They wanted raw material rather than discussion of the meaning of data.

Palmer and Kennedy (1931) had expressed the efficiency of food utilization for growth in rats as the quotient

$$\left(\frac{\text{food consumed}}{\text{gain in weight x weight}}\right)$$

In order to show that this efficiency quotient gave erroneous results, I made a mental experiment.

I calculated gain and food consumption of a small animal and one 100 times as heavy so that both gained 37 grams per 100 grams of dry food consumed. Their total weight efficiency was thus exactly equal, but the Palmer-Kennedy efficiency quotient made the larger animal 100 times as efficient as the smaller.

This calculation is shown in Slide 16 - (Efficiency for growth in small and large animals and Palmer-Kennedy quotient.)

2. Partial Efficiency. By partial efficiency I mean the quotient of a part of the gain and the corresponding part of the food consumed.

$$e_p = \frac{\Delta G}{\Delta I}$$

As in the equation above G means gain, and I food intake.

If we can make the part as small as we want then we can call the partial efficiency "differential efficiency".

$$e_p = \frac{dG}{dI}$$

Δ G may, however, also become as large as G itself and then the corresponding Δ I is the difference between the total food and the maintenance requirement. The partial efficiency then becomes what Brody calls "Net Efficiency" (1945, p. 10). He uses the latter term, however, also for another quotient namely (1945 p. 38):

$$\frac{\text{Work accomplished}}{O_2 \text{ consumed during work} - O_2 \text{ consumed during rest}}$$

Brody's term, net efficiency, is not synonymous with partial efficiency. His net efficiency is a special case of partial efficiency.

Kellner assumed that the partial efficiency was independent of the level of food intake. Armsby (1922) recognized a slightly lower partial efficiency above maintenance than below maintenance. He writes:

> The net energy values of feeding stuffs for fattening would tend to be lower than those for maintenance. Such data as are available, however, do not appear to indicate that this difference is a considerable one in the case of farm animals.

Forbes (1928) and his co-workers noted, however, a rather consistent increase of the heat increment per lb. food intake with increasing plane of nutrition. Wiegner and Ghoneim (1930) tried to apply Mitcherlich's formulation of the law of diminishing returns to the relation

of partial efficiency and plane of nutrition. Brody and Proctor (1933) discuss this in their Bul. 193. Wiegner and Ghoneim apparently missed an important difference between a field tested with increasing doses of a fertilizer and an animal offered increasing amounts of feed. The feed intake of the animal is limited by a rather efficient regulator. If you offer the animal more and more feed it will reject a larger and larger percentage, and if you then related the feed effect to the feed offered, you presumably would find the law of diminishing returns like in a fertilized field. But when you relate the effect to the feed eaten and especially to the feed digested the relation may be different. The argument of Wiegner and Ghoneim that the productive capacity of an animal is limited is correct, but they overlooked the possibility that also the oxydative capacity is limited. This limitation may maintain the food intake within a range in which the partial efficiency is constant.

3. Regulation of food intake - This regulation is shown in the hydraulic scheme (Kleiber 1936) Slide 17, which represents an early combination of two modern theories of control of food intake, Mayer's (1953) chemostatic principle and Brobeck's (1948) thermostatic principle.

The application of the law of diminishing returns to the utilization of metabolizable feed energy for animal production is thus theoretically not as well justified as it may have appeared to Wiegner and Ghoneim (1930), and also to Brody and Proctor (1933) when they discussed this application. The empirical justification is not impressive. Wiegner and Ghoneim (l.c.p. 277) write that the logarithmic interpolation (of the relation between energy in the product and energy in the feed) is not worse than the linear interpolation. If this is the case and if we have no strong theoretical reason to prefer the logarithmic interpolation, why abandon Armsby's and Kellner's simpler hypothesis that the partial efficiency of energy utilization is independent of the plane of nutrition, at least in the range above maintenance. This is, in fact, what Marston (1948) later found in his respiration trials with sheep.

For the time being we therefore are justified to maintain the simple hypothesis that partial efficiency does not consistently change with the plane of nutrition. (M. Kleiber, 1954)

We use this simplifying approximation in our discussion on the relation of total and partial efficiency.

C. The relation of total and partial efficiency

Total efficiency expresses the success of animal feeding in terms of energy. This success depends partly on the partial efficiency which is an expression for the nutritive content of the food. The success depends also on the quality of the animal as a food utilizer and the art of the herdsman to bring out this quality. To get a clear understanding of the interrelation of these influences, we formulate total efficiency in terms of partial efficiency as follows:

$$\text{Total efficiency } e_{tot} = \frac{G}{I} \quad \ldots \quad 1$$

where e_{tot} = total efficiency; G = gain; I = food intake

If we accept a constant partial efficiency e_p then we can express the gain as follows:

$$G = e_p (I - M) \quad \ldots \quad 2$$

where e_p = partial efficiency M = maintenance requirement

The gain is proportional to the difference between the total food intake I and the Maintenance requirement M.

Kellner called this difference "Productionsfutter". Using the result of equation 2 we find:

$$e_{tot} = \frac{G}{I} = e_p \frac{I-M}{I} = e_p \left(1 - \frac{M}{I}\right) \quad \ldots \quad 3$$

Assuming that the partial efficiency for maintenance is the same as that for production we can express the maintenance requirement, M, in terms of the basal metabolism, B. Without food the animal loses B calories of chemical energy from its body. This amount is saved by M calories of food energy. The amount saved is the partial efficiency times the amount fed.

$$B = e_p M \quad \ldots \quad 4$$

therefore $M = \frac{B}{e_p}$

If we introduce this expression for M into equation 3, we get

$$e_{tot} = \frac{G}{I} = e_p \left(1 - \frac{1}{e_p} \frac{B}{I}\right) = e_p - \frac{B}{I} \quad \ldots \quad 5$$

The total efficiency is the difference between the partial efficiency and the ratio of basal metabolic rate to energy intake.

D. Total Efficiency and Body Size

Equation 5 indicates that with the same partial efficiency two animals, say a large and a small one, are equally good food utilizers if their ratio B/I is the same. That means also if the reciprocal $\frac{I}{B}$ is the same, I/B is the energy intake per unit of basal metabolic rate. We have seen above that we can estimate the basal metabolic rate from the body weight as follows:

$$B = 70 W^{3/4} \quad \ldots \quad 6$$

Introducing this relation into equation 5 leads to

$$e_{tot} = \frac{G}{I} = e_p \frac{70 W^{3/4}}{I} \quad \ldots \quad 7$$

or

$$\frac{G}{I} = e_p - \frac{70}{I/W^{3/4}} \quad \ldots \quad 8$$

$I/W^{3/4}$ is the energy intake per unit of metabolic body size - the relative food intake.

We can therefore formulate:

Large and small animals are equally good food utilizers if with the same partial efficiency they take in the same amount of feed energy

per unit of metabolic body size. ($W^{3/4}$)

If partial efficiency is independent of the plane of food intake then the maximum total efficiency is reached when the animals are fed to capacity and we can then say that:

With equal partial efficiency large and small animals are equally good food utilizers if they have the same relative feed capacity, (the maximum energy intake per unit of the metabolic body size).

Slide 18 shows differences in the relative food capacity of different animals as expected but it also shows that these differences are not related to body size and we can, therefore, reach the following conclusion.

Since neither partial efficiency nor relative food capacity are consistently related to body size the total efficiency of food utilization is independent of body size. Jean Mayer (1949) has called this generalization Kleiber's law. That furnished an orderly set of pegs, and Brody and his coworkers provided a lot of experimental data to hang on these pegs.

Brody and Proctor (1935) and Brody and Cunningham (1936) showed that the energetic efficiency of lactation in Jerseys and Holsteins is about the same. Brody (1938) found also that goats produce milk with the same efficiency as cows and Brody and Nisbet (1938) even compared lactating rats with cows and concluded that the energetic efficiency of rats in the flush of lactation is within the limits found for cows; not ordinary cows but the champions among Jerseys and Holsteins! These rats produced milk with a gross (or total) efficiency of 44 to 48%.

E. Relative Production Capacity

From equation 5 we can derive the following formulation for gain:

$$G = e_p I - B \quad \ldots\ldots\ldots\ldots 9$$

That equation says that the gain is equal to the net energy in the feed minus the basal heat production.

We can divide both sides by body weight and get:

$$\frac{G}{W} = e_p \frac{I}{W} - \frac{B}{W} \quad \ldots\ldots\ldots 10$$

The gain per unit weight not only depends on the food intake per unit weight but also on the basal metabolic rate per unit weight. This latter term, as we know, decreases with increasing size of the animal. Therefore, gain per unit weight also changes with body size. We are searching for a relative gain which is not affected by size. We must, therefore, choose the last term so that it is independent of body size. We can achieve this by dividing equation 9 by B and write:

$$\frac{G}{B} = e_p \frac{I}{B} - 1 \quad \ldots\ldots\ldots 11$$

Brody and Nisbet (1938) conclude in their paper on the efficiency of milk production in rat and cow that the rat produces daily about

200 kcal milk energy per kg of body weight, a very good cow only 25 kcal/kg. But the ratio $\frac{G}{B}$ is about 2 for both rat and cow and Slide 19 gives the relative capacity of rats and cows.

Brody and Nisbet state:

> Rats like cows tend to produce about twice as many milk calories as basal metabolism calories.

Using this figure we may conclude that in rats as well as in good dairy cows the total energy efficiency for lactation is 2/3 of the partial efficiency.**

If the partial efficiency of the metabolizable energy for milk production is 60%, then the total efficiency is 40%, the highest efficiency in animal production.

We can replace B in eq. 11 by $70W^{3/4}$ and obtain the equation:

$$\frac{G}{W^{3/4}} = e_p \frac{I}{W^{3/4}} - 70 \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad 12$$

The relative production rate is a linear function of the relative food intake. The maximum relative production rate, or the relative production capacity, $\frac{G\ max}{W^{3/4}}$, is an important criterion for juding animals in the effort to breed the most efficient food utilizers.

If we select cows for the pounds of butter fat or pounds of milk or milk energy per year we are bound to breed bigger and bigger cows, but not necessarily more efficient cows. And if we select cows for milk energy per unit of body weight, we shall breed smaller and smaller cows, but again not necessarily more efficient cows. If we want to breed cows for efficiency of food utilization, independent of size, we have to select them for the highest relative production capacity; that is milk yield per unit of the metabolic body size, for example, yearly milk energy/$W^{3/4}$.

The empirical establishment of the best fitting size unit for lactation rate within one herd of cows is a practically hopeless task.

**From equation 5:

$$\frac{G}{I} = e_p - \frac{B}{I}$$

if $B = \frac{1}{2} G$ then

$$\frac{G}{I} = e_p - \frac{1}{2} \frac{G}{I}$$

or $$\frac{3}{2} \frac{G}{I} = e_p$$

$$\frac{G}{I} = \frac{2}{3} e_p$$

One obstacle is the great number of cows necessary to establish a significant difference between the prediction based on proportionality to weight and on that based on $W^{3/4}$. I have calculated that for a significant difference between the two predictions, assuming a standard error of $\pm$ 10% and a mean weight of the light half of the herd of 900 pounds and that of the heavier half of 1100 pounds, it would take 256 cows. (Kleiber and Mead, 1945)

But another obstacle is even more serious. To test the effect of size on large and small cows we have to use cows with the same "inherited impulse for milk production" as Brody calls it. (Brody and Nisbet, 1938). This impulse is always combined with the influence of size on production rate and the only way to disentangle this situation is to arrive at one variable in an independent fashion. This we can do by postulating that large and small cows have the same inherited ability for milk production if with the same relative intake of the same feed their relative rate of milk production (milk energy/$W^{3/4}$) is the same. It is exactly this inherited ability for which we ought to select breeding animals for efficient food utilization.

F. Steer and Rabbits Again.

Biologists know that smaller animals waste more energy per unit weight than large animals, and that they should, therefore, be less efficient as food utilizers.

Slide 20 illustrates the answer to that problem.

True, 300 rabbits waste 4 times as must heat per day as the steer, but they waste it only during 30 days during which they eat up the ton of hay and produce 240 pounds of meat, whereas the steer requires 120 days to eat the ton of hay. He wastes during these 120 days just as much as the rabbits waste during 30 days and the steer produces in 120 days 240 pounds of meat which is as much as the 300 rabbits produce in 30 days. If you like feeding you may say you prefer the steer because you can enjoy him 4 times as long as you can enjoy the 300 rabbits.

IV CONCLUSION

Metabolic rate, food utilization, and body size comprise just one segment of Samuel Brody's wide range of activities and accomplishments as a research worker. In concluding this lecture I want to tell you again how grateful I am for this opportunity to discuss especially my personal relation with Brody as a fellow scientist, a cooperation between one who was especially gifted with what it takes to increase our knowledge with new facts and ideas and the other especially concerned with critical evaluation of theories.

Brody's fertile mind full of ideas, combined with his energy and his talent for organizing experimental research, has led to a great amount of new information. His enthusiasm has made research more exciting for his students and co-workers; his humor has made meetings more pleasant for his fellow scientists; his friendliness has made life more enjoyable for all who knew him.

We are grateful that Samuel Brody has been with us.

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SLIDE 1 SURFACE AREA OF A RAT

Measured by H. H. Mitchell (J. Nutr. 2: 441, 1930)

Weight of rat	413 g.
Surface area:	
Skinned carcass (Mold)	430 cm^2
Unstretched skin	536 cm^2
Moderately stretched skin	630 cm^2

Note: ($10 \times W^{2/3} = 5.56\ dm^2 = 566\ cm^2$)

SLIDE 2 FORMULATING ALLOMETRIC SURFACE AREA

Example - Mitchell's Chickens, J. Nutr. 2: 447 (1930)

$$S = 8.19\ W^{.705} = 10.6\ W^{2/3} \times \frac{8.19}{10.6}\ W^{0.038}$$

isometric size effect; factor for allometry

Weight grams	Surface area calculated		factor for allometry
	Mitchell allometric	Meeh isometric	
	$S = 8.19\ W^{.705}$	$S = 10.6\ W^{2/3}$	$\frac{8.19}{10.6}\ W^{0.038}$
100	210	229	0.916
1000	1067	1060	1.001
2000	1739	1685	1.028

SLIDE 3 RAT SURFACES IN 1943

(M. Kleiber. Ann. Rev. Physiol. 6: 125, 1944)
10 papers from 8 laboratories published in one year

Papers	Formula for calculating surface area	Units of Weight
4	not given	W
1	$S = 7.42 \times W^{2/3}\ dm^2$	kg
1	$S = 9.1 \times W^{2/3}\ dm^2$	kg
1	$S = 10 \times W^{2/3}\ dm^2$	kg
1	$S = 12.44 \times W^{3/5}\ dm^2$	kg
2	$S = 0.001\ W^{0.63}\ m^2$	g

SLIDE 4 THE BLOODY RAT

Animal	Body Weight	Blood %	Blood Wt. per unit area
	W	$\frac{B}{W}\ 100$	$\frac{B}{W} \cdot W^{1/3}$
Man	70 kg	4.9%	$0.049\ W_m^{1/3}$
Rat	70 g	100 x	$x \cdot W_r$

If $x \cdot W_r^{1/3} = 0.049\ W_m^{1/3}$

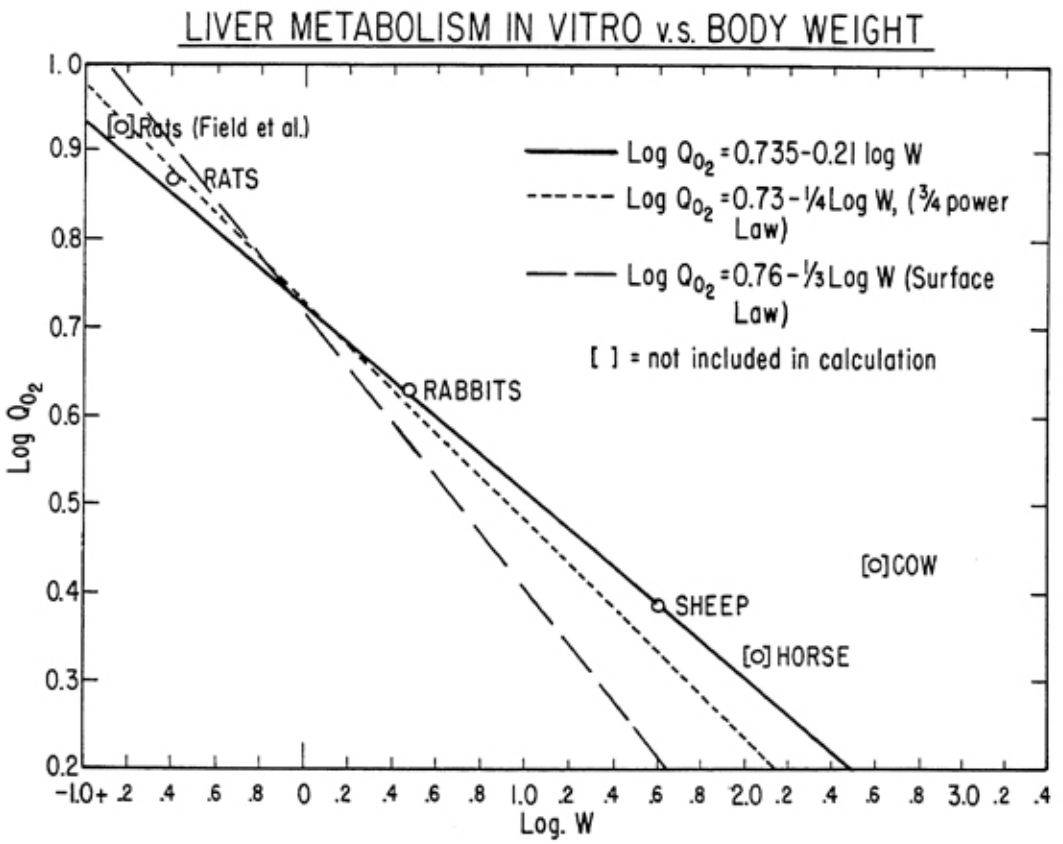
then $x = 0.049 \frac{W_m^{1/3}}{W_r} = 0.49 = 49\%$ blood

SLIDE 5 BLOOD VOLUME AND BODY WEIGHT

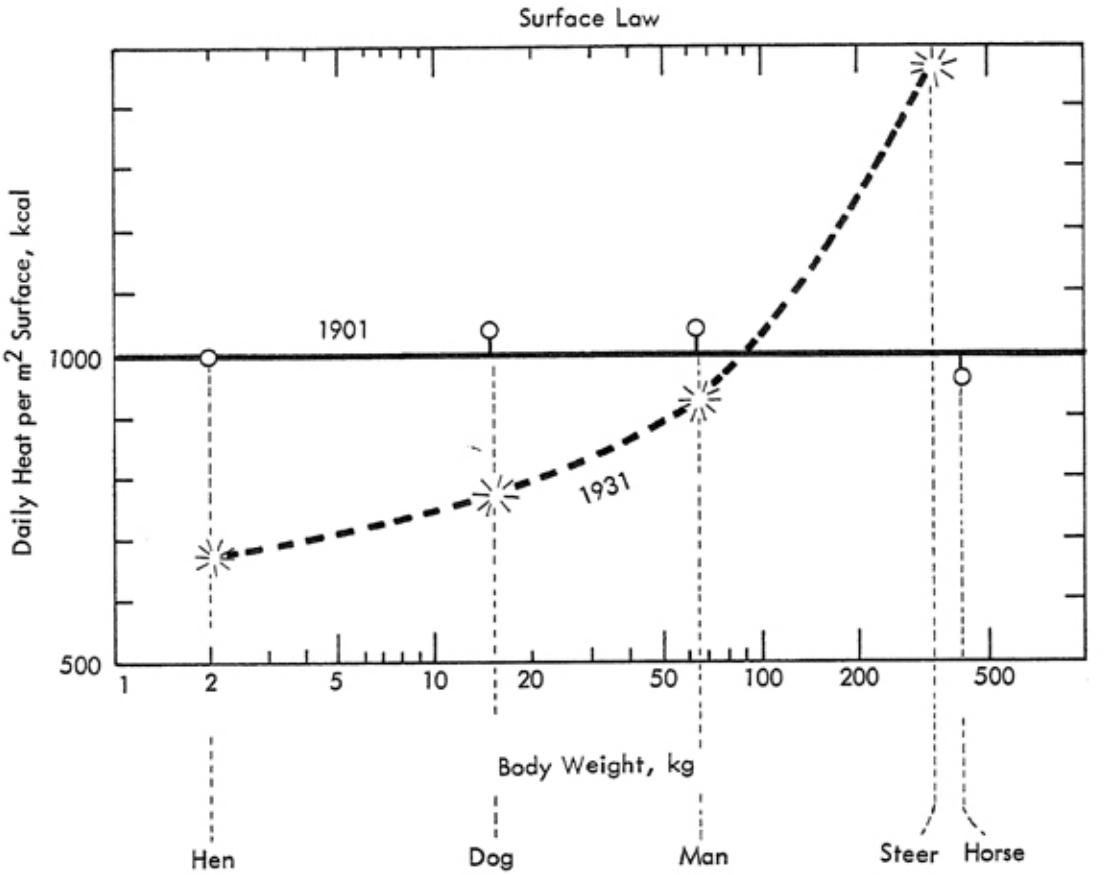
Animal	Sources of formulas	Body Weight, Grams (W)	Blood volume cc	Blood quantity in percent of body weight
1	2	3	4	5
Rabbit	*Average of 22 determinations, table 1, p. 138	670-3,250	$0.632\ W^{2/3}$	4.92
Guinea pig	Average of 9 determinations, table 16, p. 152	215-825	$0.189\ W^{2/3}$	4.10
Mouse	Average of 19 determinations, table 20, p. 154	11.9-29.3	$0.149\ W^{2/3}$	5.77

*Data of G. Dreyer and W. Ray. Phil. Trans. Roy. Soc. B, vol. 201: 133-160 (1910)

SLIDE 6

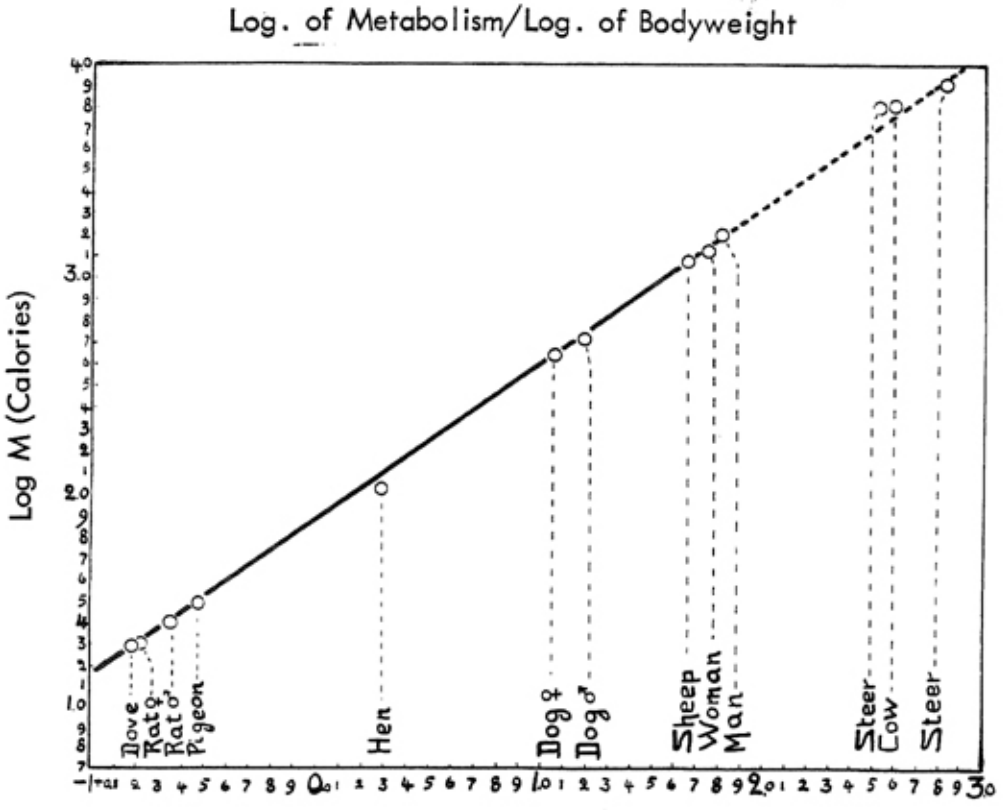


SLIDE 7



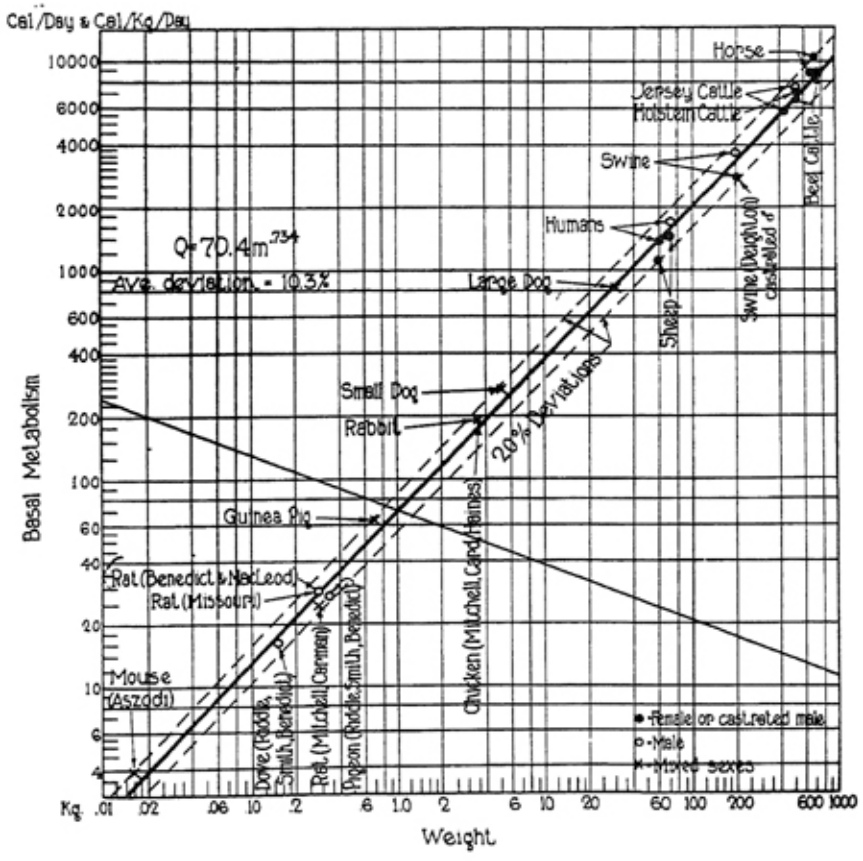
1901: Data of Voit - cit by Krogh, Resp. Exch. 1916 p. 142
1931: Data of American Invest. cit by Kleiber, Hilgardia 1932

SLIDE 8

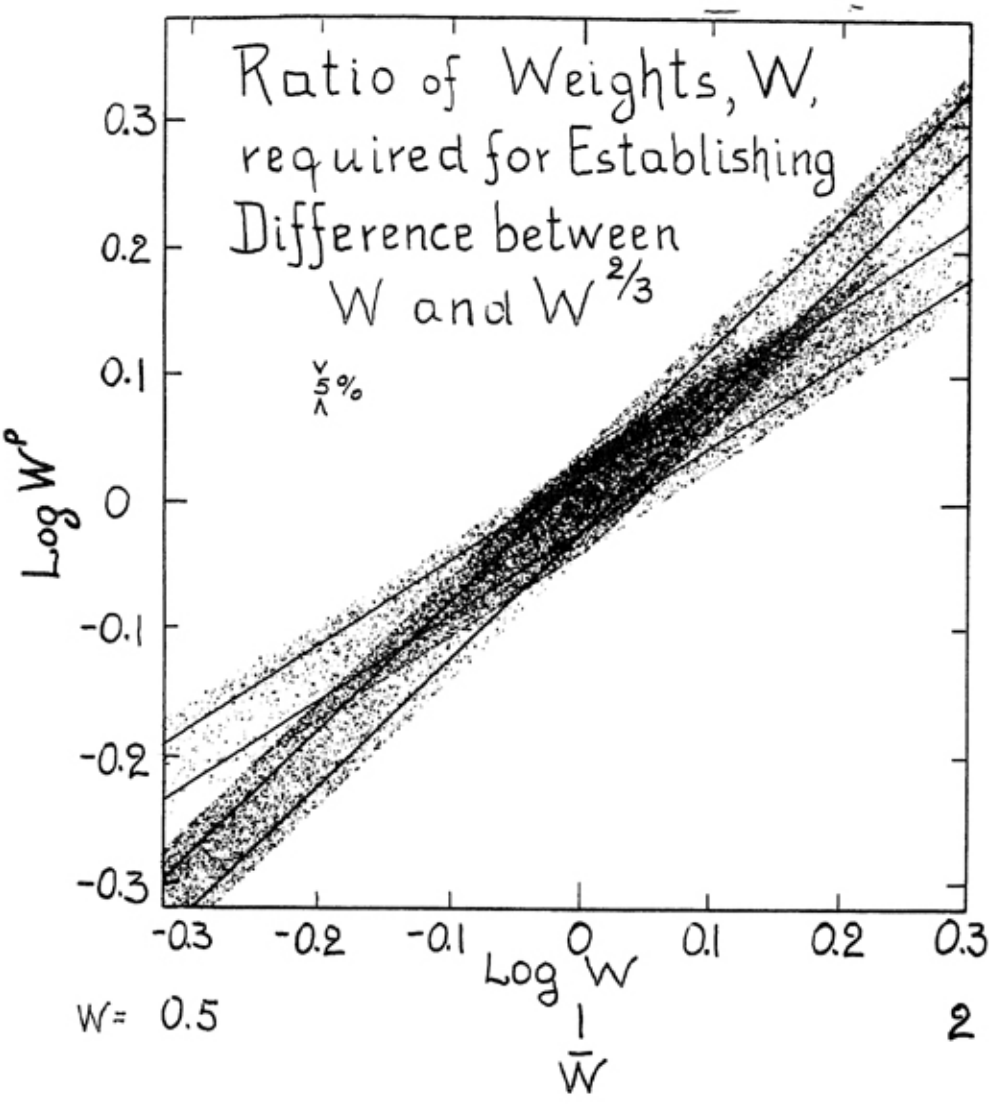


Log M = 1.872 + 0.726 Log W (excluding Ruminants)
The diameter of circles covers a deviation of ± 5%

SLIDE 9

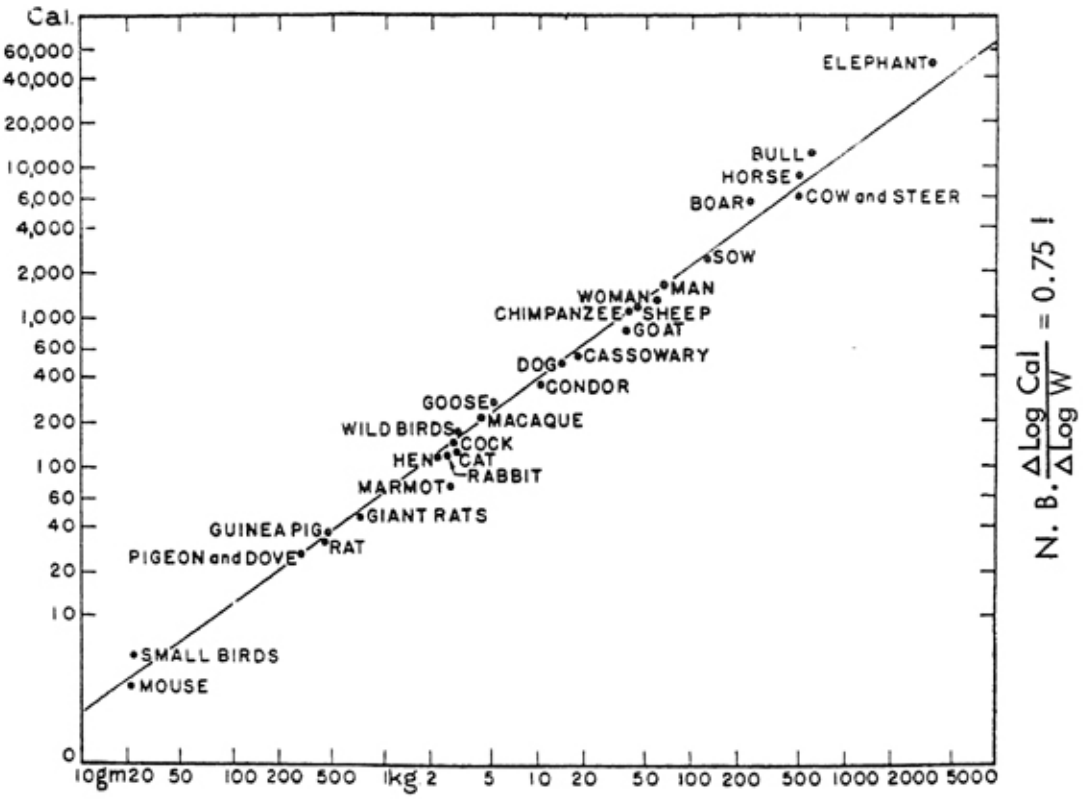

Cal./Day & Cal./Kg./Day
Basal Metabolism
Weight
Kg.
Q=70.4m^.734
Ave. deviation = 10.3%
20% Deviations
Horse
Jersey Cattle
Holstein Cattle
Beef Cattle
Swine
Humans
Large Dog
Sheep
Swine (Dough,Lot) castrated &
Small Dog
Rabbit
Guinea Pig
Rat (Benedict & McLeod)
Rat (Missouri)
Mouse (Aszodi)
Dove (Riddle, Smith, Benedict)
Rat (Mitchell, Carman)
Pigeon (Riddle, Smith, Benedict)
Chicken (Mitchell, Card, Haines)
Female or castrated male
Male
Mixed sexes

SLIDE 10

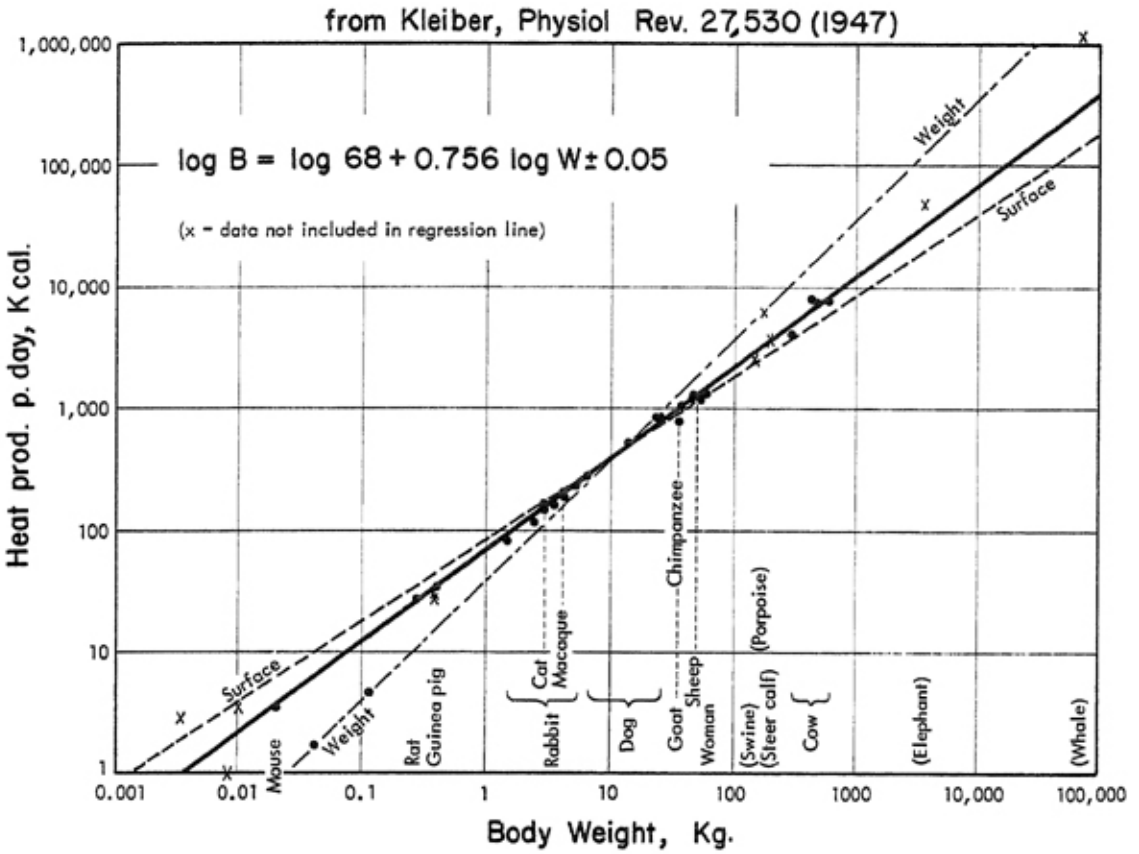

Ratio of Weights, W,
required for Establishing
Difference between
W and W 2/3
5%
Log W^p
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.3
-0.2
-0.1
0
0.1
0.2
0.3
Log W
W= 0.5
1
2
W̄

SLIDE 11

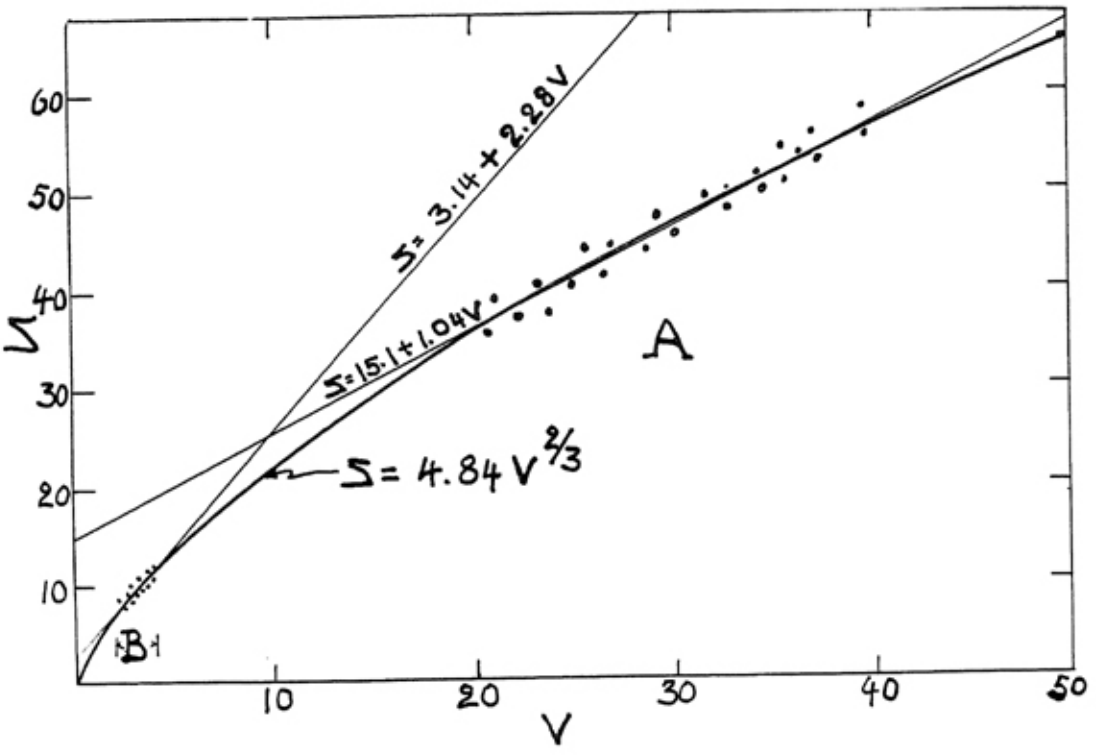
From Benedict Vital Energetics 1938, 171



SLIDE 12


from Kleiber, Physiol Rev. 27,530 (1947)
log B = log 68 + 0.756 log W ± 0.05
(x = data not included in regression line)
Heat prod. p. day, K cal.
Body Weight, Kg.
1,000,000
100,000
10,000
1,000
100
10
1
0.001
0.01
0.1
1
10
100
1000
10,000
100,000
Weight
Surface
Surface
Weight
Mouse
Rat
Guinea pig
Rabbit
Cat
Macaque
Dog
Goat
Chimpanzee
Sheep
Woman
(Swine)
(Steer calf)
(Porpoise)
Cow
(Elephant)
(Whale)

Slide 13
Surface area and Volume of Spheres



SLIDE 15 PARTIAL EFFICIENCY OF FEED UTILIZATION AND BODY SIZE

$$e_p = \frac{\text{Energy in produced body fat}}{\text{Metabolizable energy in production food}^{1)}} 100$$

Food	Rabbit Observed[2)]	Steer Calculated[3)]
	%	%
Green Corn Plants chopped	78	48
Dried Corn Plants Chopped	39	35
Dried Corn Plants Chopped and then soaked in Water	46	45
Dried Corn Plants Ground and then Soaked in Water	40	45
Dried Corn Plants Ground and then Soaked in Water	57	46

1) Production food = Total food minus maintenance requirement.

2) M. Kleiber. Habilitation Thesis. ETH, Zurich, 1927.

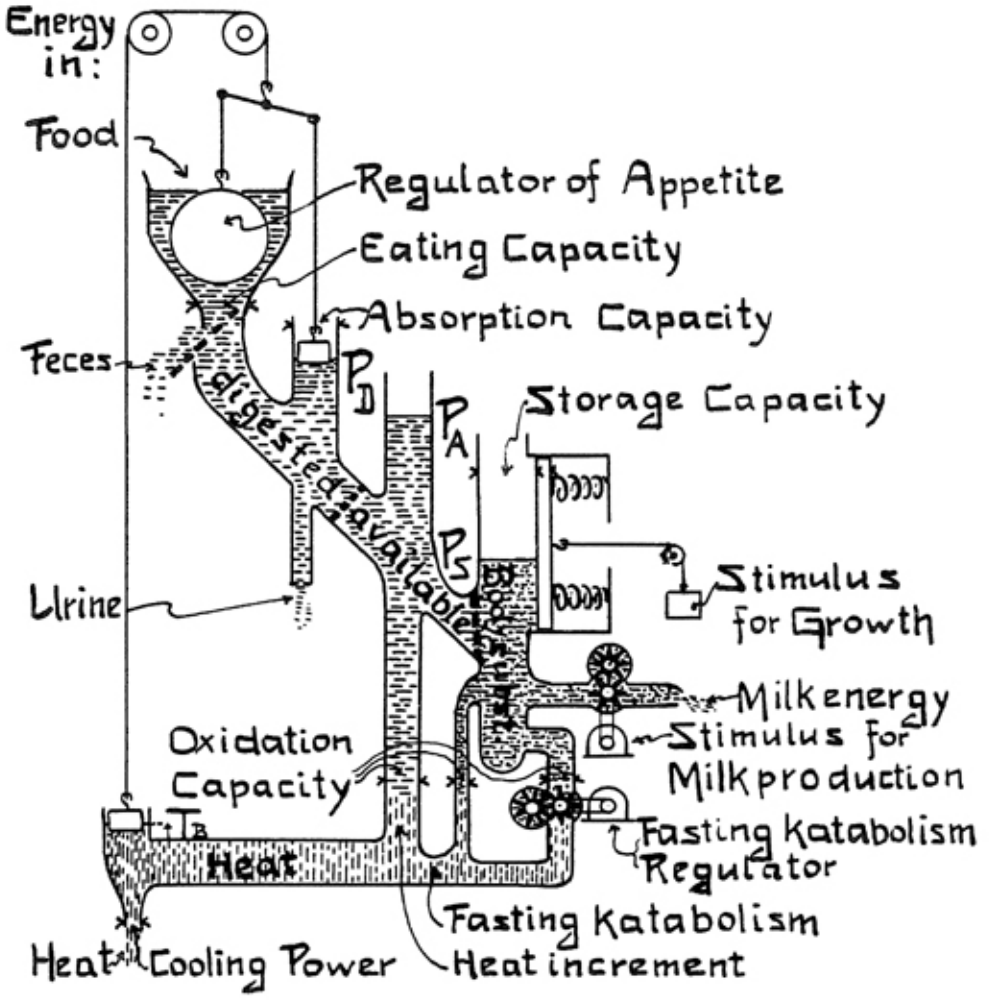
3) Calculated from chemical composition and digestibility according to Kellner (1919).

SLIDE 16 WEIGHT EFFICIENCY FOR GROWTH AND BODY SIZE

	Baby Chicks Observed	Larger Animals Calculated
Body weight	65 g	6.5 kg.
Metabolic body size, $W^{3/4}$	.129 $kg^{3/4}$	4.07 $kg^{3/4}$
Daily gain in weight	3 g	94.5 g
Daily dry food total	8.73 g	275.0 g
Daily dry food for maintenance	4.68 g	147.4 g
Daily dry food for production	4.05 g	127.6 g
Partial Efficiency $\frac{\text{Gain}}{\text{Food for Production}} 100$	74%	74%
Total Efficiency $\frac{\text{Gain}}{\text{Total Food}} 100$	34%	34%
Palmer-Kennedy efficiency quotient		
$\frac{\text{Total Food}}{\text{Gain x Body Weight}}$	4.5	0.045

Slide 17

Scheme of Energy-Utilization



SLIDE 18 RELATIVE FOOD CAPACITY vs. BODY SIZE*

Animal	Body Weight	Maximum Daily Intake of food energy per Animal	Maximum Daily Intake of food energy per unit of metabolic body size	Daily energy loss during fasting	Relative food capacity
	W kg	U kcal	$\frac{U}{W^{3/4}}$	per $kg^{3/4}$ kcal	$\frac{U}{B}$
Chick	0.078	53.5	360	81	4.4
Rabbit	2.36	480.	253	50	5.1
Sheep	50.	5730.	305	69	4.4
Swine	130.	13980.	363	64	5.7
Steer	427.	42429.	452	81	5.6
Steer	444.	36026	373	88	4.2

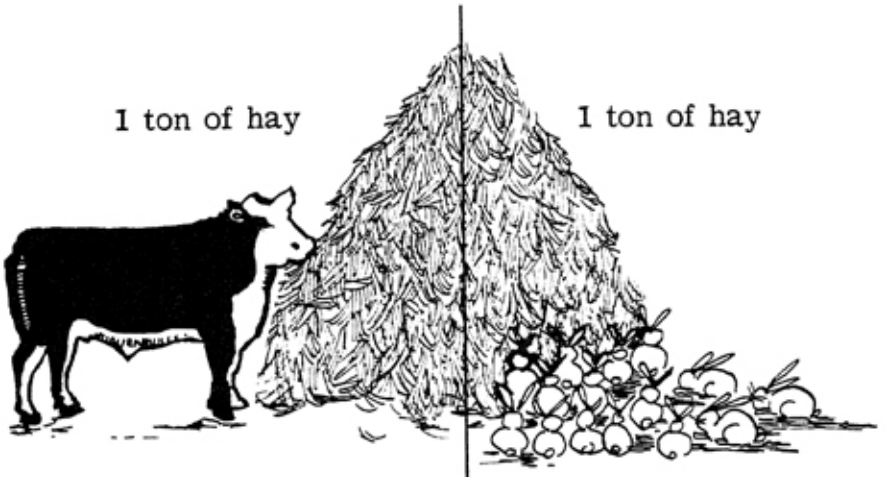
*Kleiber, M. Tiergrosse und Futterverwertung. Tierernahrung 5: 1-12 (1933)

SLIDE 19 RELATIVE LACTATION CAPACITY

Energy in Milk per unit of Metabolic Body Size $W^{3/4}$

	$kcal/kg^{3/4}$
Superior cows all breeds	120
Champion Holstein	266
Champion Jersey	360
Rat lowest (5 babies)	118
Rat highest (9 babies)	203
Rat mean	148

Data from S. Brody and Ruth Nisbet. Missouri Research Bulletin 285, 1938.



Animals	1 steer	300 rabbits
Body weight total	1,300 pounds	1,300 pounds
Food consumption per day	16-2/3 pounds	66-2/3 pounds
One ton of hay lasts	120 days	30 days
Heat loss per day	20,000 kcal	80,000 kcal
Gain in weight per day	2 pounds	8 pounds
Gain from one ton of hay	240 pounds	240 pounds

Slide 20 --Food Utilization Versus Body Size

M. Kleiber, Elements of Animal Nutrition 1948