

GROWTH AND DEVELOPMENT

With Special Reference to Domestic Animals

- XVII. Relation Between *Resting* Energy Metabolism and Body Weight in Growing Domestic Mammals. Samuel Brody, W. C. Hall, A. C. Ragsdale and E. A. Trowbridge.*
- XVIII. Relation Between Basal Metabolism, Resting Metabolism, Heat Increments of Feeding and Body Weights in Growing Farm Mammals. Samuel Brody, W. C. Hall, A. C. Ragsdale, and E. A. Trowbridge.*
- XIX. Relation Between Basal Metabolism and Body Weight in the Growing Domestic Fowl. Samuel Brody, E. M. Funk, H. L. Kempster.
- XX. Relation Between Basal Metabolism and Body Weights in the Growing Rat. U. S. Ashworth, Samuel Brody, and A. G. Hogan.
- XXI. Relation Between Basal Metabolism and Body Weight in Man; Published Data. Samuel Brody and R. C. Procter.
- XXII. Relation Between Basal Metabolism and Body Weight in Laboratory Animals; Published Data. Samuel Brody, R. C. Procter.
- XXIII. Relation Between Basal Metabolism and Mature Body Weight in Different Species of Mammals and Birds. Samuel Brody and R. C. Procter.

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FOREWORD

The special investigation on growth and development is a cooperative enterprise in which the departments of Animal Husbandry, Dairy Husbandry, Agricultural Chemistry, and Poultry Husbandry have each contributed a substantial part. The plans for the investigation in the beginning were inaugurated by a committee including A. C. Ragsdale, E. A. Trowbridge, H. L. Kempster, A. G. Hogan, F. B. Mumford. Samuel Brody served as chairman of this committee and has been chiefly responsible for the execution of the plans, interpretation of results and the preparation of the publications resulting from this enterprise. Other members of the staff who have made contributions are: D. W. Chittenden, J. E. Comfort, and F. F. McKenzie.

The investigation has been made possible through a grant by the Herman Frasch Foundation represented by Dr. R. W. Thatcher, who has given valuable advice from the beginning of the investigation. The National Research Council has also participated in the investigations by a grant for which acknowledgment is hereby made.

F. B. MUMFORD, *Director Agricultural Experiment Station*

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GROWTH AND DEVELOPMENT

With Special Reference to Domestic Animals

XVII. Relation Between Resting Energy Metabolism and Body Weight in Growing Domestic Mammals.*

ABSTRACT

1. This paper presents data for *resting* energy metabolism of dairy and beef cattle, sheep, horses, and swine from birth until about 3 years of age. The metabolism was measured before the regular morning feeding, which is 8 to 12 hours after the preceding regular evening feeding while the animals were in their normal lying (haunches) position. The metabolism thus measured is termed *resting* metabolism to differentiate it from *basal* metabolism measured in a similar resting, but also in post-absorptive condition. Since the *resting* metabolism includes the heat increment of feeding, it is taken to be identical with the maintenance needs of the resting animal for metabolisable energy under the given conditions. The metabolic rate is computed from the rate of oxygen consumption.

2. Evidence is presented showing the impracticability of using surface area as a unit of reference for purposes of comparing the metabolism of different species. In this paper the metabolism during growth is related instead to weight by the exponential equations $Q/m = Ae^{-km}$ or $Q/m = Ae^{-km} + C$, in which Q is the heat production for weight m , and C is the lowest or limiting value for Q/m . This equation is of the same general form as the one representing rates of growth, rates of senescence and rates of decline of the nucleo-cytoplasmic ratio with increasing weight during growth.

3. The metabolic rates of pregnant animals are above the general level indicated by the equations. The metabolism of lactating animals is still higher above the general metabolic level.

4. Other conditions being the same, the lightest feeders have the lowest *resting* metabolism, and the heaviest feeders have the highest metabolism.

5. Dairy cattle males have a 10 per cent higher metabolic level than females; swine males have a 20 per cent higher metabolism than females; castrated males in cattle and swine have the same metabolism as females if conditions of feed intake are the same.

6. While our female beef animals have a slightly lower metabolism than female dairy animals, this difference is probably due to differences in food intake and not to breed differences as such.

INTRODUCTION AND DEFINITIONS

Since the publication of the preceding report on metabolism (Missouri Research Bulletin 143), much additional data have been accumulated by the use of the method previously described, bringing most of our animals to age three years. It seems that the data have become sufficiently extensive to justify the formulation of a rational equation relating energy metabolism to increasing weight during growth. The present report is devoted to this purpose, and to the presentation of the data, chiefly in the form of charts.

We have called attention in the preceding report to the great importance of a knowledge of the maintenance metabolism in the estimation of the efficiency of growth and related transformations: It is not possible to compute the efficiency of such processes unless proper correction is made for the cost of maintenance of the animal. This is the *economic* reason for giving this much attention to the problem of maintenance metabolism.

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Maintenance metabolism may be subdivided into (1) *basal* metabolism, that is, energy metabolism when the animal is at rest and in post-absorptive condition; and (2) *resting metabolism* differing from basal metabolism only in that the animals are not in post-absorptive condition. The resting metabolism measurements are made in the morning, before the morning feeding, which is 10 to 12 hours following the preceding regular evening feeding. The milking cows, however, were fed late in the evening, so that in the latter case, the morning measurements are nearer 7 or 8 hours after the preceding evening feeding. The present report is concerned not with the *basal*, but with the *resting* metabolism data as thus defined. The following paragraphs are intended to give a more detailed insight into the significance of and the relation between *resting* metabolism and *basal* metabolism.

The concept of basal metabolism as regards humans is fairly simple. It is the energy expended for the maintenance of the completely resting organism, about 12 hours after a normal meal. It is a daily occurrence in most humans, as for example at the time of waking in the morning. Metabolism measured less than about 12 hours after feeding is not basal because then additional heat is produced consequent to ingestion of food. This additional heat may be termed the *heat increment of feeding*. Basal metabolism, then, does not include the heat increment of feeding; it is attained in humans about 12 hours after feeding; and it is an altogether normal and daily occurrence in humans.

But in farm animals, especially in ruminants, we have a different situation. Digestion and absorption in these animals are relatively slow processes. It takes 2 to 4 days to reach the post-absorptive condition; and normally they never reach it, as they are normally fed at least every 12 hours. Instead of the metabolism fluctuating up and down in a cyclic manner following each feeding, as in the case of humans, the resting metabolic rate of ruminants under usual conditions of feeding remains at a practically constant level throughout the day, and from day to day. This relatively *constant metabolic level* in ruminants (and to a less extent in other farm animals) includes the heat increment of feeding. Our resting metabolism data represent this practically constant metabolic level of the resting organism, including the relatively constant heat increment of feeding.

A question that naturally arises in this connection concerns the relation between the feed energy needs of the animal for maintenance and the resting metabolism data as here presented.

One way to answer this question is to investigate mathematically the relation between the metabolism values as here recorded and the feed energy consumed by the animal under the same conditions. This investigation we reserve for the future.

But for the present purposes it is more interesting to define the resting energy metabolism in terms of the metabolisable energy of foodstuffs needed by the animal for maintenance under the given conditions.

The metabolisable energy of a foodstuff is, of course, that part of it which after digestion enters the body proper and is there metabolized. Quantitatively, it is the gross fuel value of the foodstuff less the fuel value of the urine and feces.

The metabolisable energy as above defined differs from Armsby's net energy in the fact that the former includes the heat increment of feeding (thermic energy, or specific dynamic effect) while the latter does not. Net energy is metabolisable energy less the heat increment of feeding. The heat increment is deducted from metabolisable energy because it can not be used for productive purposes; it is in part a by-product of the intermediate metabolism, in part the energy expended by the kidneys to excrete the end products of protein metabolism, and in part the energy expense of the digestive processes.

Resting metabolism as above defined differs from *basal* metabolism in the same manner. The former includes the heat increment of feeding, while the latter does not.

If basal metabolism is taken to be quantitatively identical with the net feed energy needs for maintenance under basal conditions, then resting metabolism must be considered to be quantitatively identical with the metabolisable energy needs for maintenance of the resting animal; and this then is the practical significance and the relation, as we see it, between the data here presented and the feed needs of the animal.

It must be added that the term maintenance as used in this paper includes the energy expense of growth, gestation, milk secretion, fattening; but it does not include the energy stored in the products of these transformations.

AN EXPONENTIAL EQUATION RELATING RESTING METABOLISM WITH BODY WEIGHT DURING GROWTH

It is generally known that the energy metabolism per unit weight tends to decline with increasing weight of the animal. Thus the average daily basal metabolism of a 40 kilo man is 32 Calories per kilo; but of an 80 kilo man it is only 23 Calories per kilo. This decline is ordinarily explained by assuming that the energy metabolism is proportional not to weight but to surface area, and as the surface area per unit weight in a large animal is smaller than in a small animal, therefore the metabolism per unit weight in a large animal is smaller than in a small animal. Rubner went so far as to generalize that the metabolism per unit area

is the same in all warm blooded animals (about 1000 Calories per square meter of surface); and with a few notable exceptions Rubner's generalization has been accepted by physiologists and biochemists.

It is admitted, however, that Rubner's generalization of constancy of metabolism per unit area is not applicable to growing animals. Rubner's generalization not being applicable to growing animals, and since surface area is a derived value (computed from the body weight by means of a formula), we have decided to relate metabolism directly to weight in our (growing) animals, and thus do away with the use of a derived and often uncertain value for area.

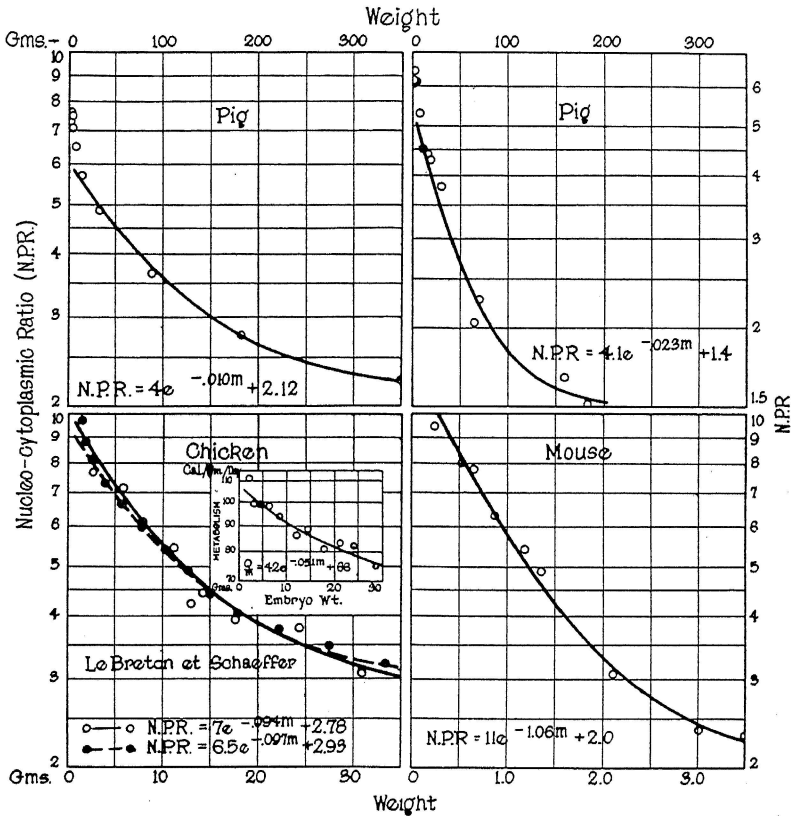


Fig. 1a.—The course of decline of the nucleo-cytoplasmic ratio with increasing weight of the embryos of three species. The chart was prepared from data published by Le Breton and Schaeffer. Equation (2) given in the text seems to fit the data satisfactorily. The inset in the lower left quadrant shows the same equation fitted to the heat production in the chick embryo. The heat production data are by Bohr and Hasselbalch, while the embryo weights are by Byerly. The classic data of Bohr and Hasselbalch were chosen because their respiratory-exchange data were checked by a direct calorimetric method. Byerly's weight data were chosen because of the standard size of eggs used, and the very extensive population on which the averages are based.

There is a more general reason against relating metabolism to surface area: There are a number of distinguished investigators who do not accept the theory that surface area is a limiting factor in the rate of basal metabolism.

Thus Benedict assumes that the rate of basal metabolism is limited, not by the surface area but by the "active protoplasmic mass" of the organism. Le Breton and Schaeffer have particularized this concept by assuming that the nucleo-cytoplasmic ratio conditions the "active mass" which limits the metabolic rate.

The investigations of Minot have made it generally known that the nucleo-cytoplasmic ratio decreases with increasing weight during growth. Indeed, he formulated an elaborate theory of growth and senescence on the basis of the decrease of this ratio during growth. Le Breton and Schaeffer have recently published chemical data for the decline of the nucleo-cytoplasmic ratio with age in very young animals.

By way of examination of the arguments of Le Breton and Schaeffer, we have investigated their data mathematically and found that the decline of what they term the nucleo-cytoplasmic ratio (*rapport nucléoplasmique*) follows an exponential course with increasing body weight of the organism.

Their data, and the exponential curve that we have fitted, are shown in Fig. 1a. To test their suggestion that the nucleo-cytoplasmic ratio might be the limiting factor in metabolism, we have also inserted (in the lower left quadrant) the weight curve of energy metabolism for the chick embryo. The classic metabolism data of Bohr and Hasselbalch were used since their energy metabolism values as obtained by the respiratory-exchange method were checked by a direct calorimetric method. The embryo weight data are by Byerly.

Fig. 1a shows that the metabolism of the chick embryo follows the same course as the nucleo-cytoplasmic ratio. However, no very broad generalization can be made upon the basis of this resemblance, for the following reasons:

1. The heat production by the incubating egg includes not only the metabolism of the embryo itself, but also of the yolk sac and of the allantois. The curve obtained by relating metabolism to the sum of the weight of the embryo and of these structures gives a curve of quite a different shape. Byerly has deducted the estimated weight of the yolk attached to the yolk sac from the yolk sac, and he found that the metabolism per unit weight of the sum of the embryo, allantois, and the corrected weight of the yolk sac is constant throughout the whole period of incubation. Such a constancy of metabolism seems quite improbable to us in the light of other experiences, and in view of this uncertainty we

believe that the problem needs a good deal more investigation before we shall be in a position to draw any conclusion concerning the apparent resemblance between the metabolism and nucleo-cytoplasmic curve.

2. Besides, any resemblance between curves might be entirely fortuitous. We are not inclined to believe that there is only *one* factor that limits basal metabolism. It is much more probable, as suggested (in personal conversation) by *M. André Mayer* and *M. L. Plantefol*, (both of the Collège de France) that the basal metabolism is a partial function of many variables, including possibly surface area, protoplasmic mass, nucleo-cytoplasmic ratio, water content, fat content, etc. And any one of these, or some other factors, might limit the rate of metabolism. According to this conception, all equations and all units of reference must be considered as more or less empiric. The writer accepts this point of view, and our present suggestion of an exponential equation is made with a full realization of its empiric nature.

As regards the use of surface area as a practical unit of reference, this may be justifiable as far as humans are concerned, chiefly on grounds of established usage, but also because the formula relating area to weight seems to have been established with much precision or at any rate it is widely accepted.

But this is not true as regards farm or laboratory animals. We may take, for example, the case of the white rat. Three investigators have recently published data on the area of this species. We have plotted these three sets of data on a logarithmic grid in Fig. 1b. The results are that no two data sets agree; and the average difference between two of the sets is over 60 per cent! What is the use of relating metabolism to a unit of reference which varies by over 60 per cent when measured by different investigators? Why not relate it to weight which can be measured uniformly by *all* workers with a precision which is greater than 99 per cent.

H. H. Mitchell (1930) who endorsed the use of surface area as unit of reference, admitted that "the surface area is not a definite measurement, but depends to a considerable extent upon the shape of the body as determined by the position of the body trunk and its appendages" and "the heat produced by an animal per square meter of body surface possesses no absolute meaning" unless "the surface measurement for different animals is made by exactly the same method". Now, as we see it, if we exclude its use for clinical purposes, the only use of surface area as unit of reference is for purposes of comparing the metabolism of different species; and it is practically impossible to measure widely different species by exactly the same method, especially—as it must be—if the measurements are made by different investigators.

This is the practical objection against the use of surface area as unit of reference at least in non-humans, regardless of theoretical implications. Besides, if metabolism is proportional to area, and area is a function of weight (or weight and height), then metabolism is likewise a function of weight (or weight and height), and there seems to be no reasonable

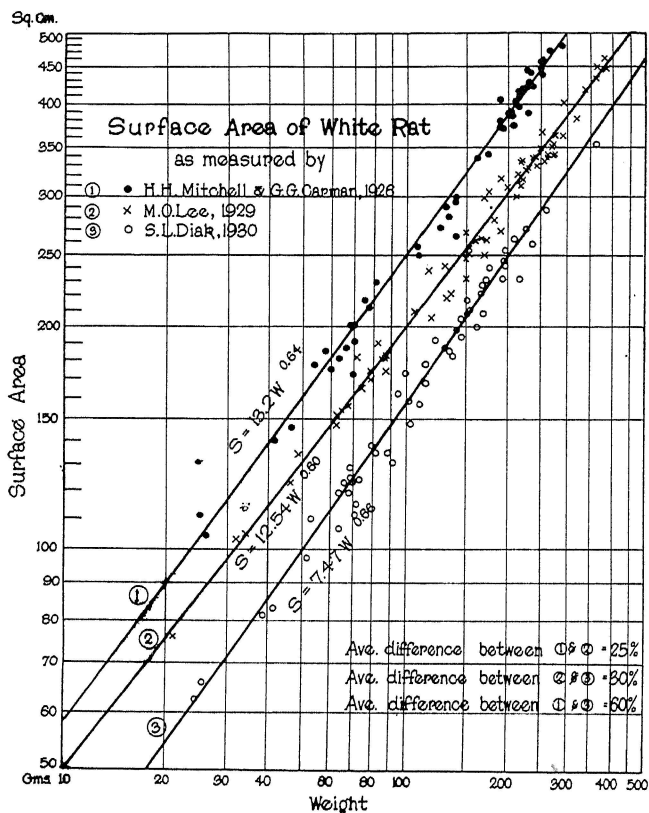


Fig. 1b.—The surface area of the white rat as found by three different investigators. Note the percentage differences between the three curves. Since the difference between Mitchell's and Diak's values on the same species are over 60%, therefore measurements by different investigators on different species are still less likely to be comparable. Furthermore, since it has not been proved that surface area is a limiting factor in the intensity of energy metabolism, would it not therefore be better to relate metabolism to weight, thus eliminating the error of derivation of area.

advantage in relating metabolism to area, which area is computed from weight, when metabolism might be related directly to weight; and especially if it has not been *proved* that area is the *limiting* factor in energy metabolism.

Having decided to relate metabolism to weight, the question remains as to what method should be used for making such a relation.

Shall we use a biometric method according to the manner of Harris and Benedict? The objection against their method is that their constants have no rational significance, and extrapolations lead to ambiguous results. Such formulae have their legitimate uses for the purposes for which Harris and Benedict used them, namely for establishing empiric metabolism standards within certain limits; but obviously they can have no usefulness in an effort for establishing *laws* of metabolism in which constants have clearly defined significance, preferably some universal significance.

The equation that we have decided to investigate to begin with is the same that we have used to represent the weight changes in the nucleocytoplasmic ratio shown in Fig. 1a; and the same general type that we have used to represent the course of growth in animals, plants and population as described in Missouri Research Bulletin 97, and also the course of senescence as described in Missouri Research Bulletin 105. Briefly the equation may be developed as follows:

Let Q represent the heat produced in the organism during a convenient time, and let m be the weight of the organism. Then, of course Q/m is the heat produced in the given time interval per unit weight. Now we have found that Q/m declines with increasing values of m at a constant percentage rate, $100k$.

In the form of an equation, this statement is written

$$Q/m = Ae^{-km} \quad (1)$$

in which, A is a parameter representing the point on the Q/m axis cut by the extrapolated curve of the equation. Equation (1) represents the data satisfactorily for relatively short periods. In case of cattle, it represents the data satisfactorily from 40 to 300 or 400 kilograms, depending on the individual; and certainly until puberty. But following puberty, a more satisfactory agreement between observed and computed values is obtained by assuming that the metabolism per unit weight declines until a certain limiting value, C , is reached. In such a case (1) is modified to

$$Q/m = Ae^{-k_1 m} + C \quad (2)$$

Equation (2) indicates that above the value C , the metabolism per unit weight, Q/m , declines with increasing weight, m , at the rate of $100k_1$ per cent for each unit weight of increase. As the limiting value C is more and more closely approached, the metabolism per unit weight, Q/m , tends to stabilize about the constant value C , and the total heat production in the animal tends to become directly proportional to body weight (i. e., $Q = mC$). If this is true, then this is a new and very im-

portant practical fact—that *beyond a certain weight, the metabolism is practically directly proportional to weight.*

The following are some important properties of equations (1) and (2):

Equation (2) if written in the form

$$Q = mAe^{-k_1 m} + Cm$$

gives on differentiation

$$\begin{aligned} dQ / dm &= Ae^{-k_1 m} - mAke^{-k_1 m} + C \\ &= (1 - km)Ae^{-k_1 m} + C \end{aligned}$$

Equation (1) on differentiation is the same as above but without the C.

A most curious property of equations (1) and (2) is that they have inflections in their curves. The weight at the inflection is obtained by differentiating a second time and equating to zero.

$$\begin{aligned} d^2Q / dm^2 &= -Ak_1 e^{-k_1 m} - (1 - mk_1)Ake^{-k_1 m} \\ &= -Ak_1 - (1 - mk_1)Ak_1 = 0 \\ &= Ak_1(-1 - 1 + mk_1) = 0 \\ \therefore m &= 2 / k_1 \end{aligned}$$

so that the metabolic rate goes through a minimum when $m = 2 / k_1$. The minima of the several sets of data are clearly shown in Fig. 10, and in Tables 1, 2, and 3. Whether this inflection is a fiction or a biological fact remains to be seen.

If we represent the ratio Q / m by R, then we get for equation (1)

$$\begin{aligned} R &= Ae^{-km} \\ dR / dm &= -kAe^{-km} \\ &= -kR \end{aligned}$$

For equation (2), we get

$$\begin{aligned} R_1 &= Ae^{-k_1 m} + C \\ dR_1 / dm &= -k_1 Ae^{-k_1 m} \\ &= -k_1(R_1 - C) \end{aligned}$$

These forms bring out the similarity between equations (1) and (2) and the well-known "mass action" equations used in physical chemistry; and show, formally at least, the possible relations that might exist between metabolism and the "active mass" as propounded by Le Breton and Schaeffer, as well as between changes in the course of metabolism with changes in the rates of growth and rates of senescence.

The arguments in favor in our proposed metabolism equation are, then, first, its rationality; rational in the sense that there is nothing ambiguous about any of its constants; the significance of each constant is clearly defined. Second, it represents also the weight changes in the "active mass" (i. e., nucleo-cytoplasmic ratio) which, according to one theory, might limit the metabolic rate. Third, it eliminates the use of the uncertain surface area as unit of reference. Fourth, our proposed equations and several of its forms after differentiation are quite familiar to the physical chemist, and physicist. This is of some advantage, as it may turn out that the metabolic rate is limited by some simple physico-chemical mechanism similar to those known to occur in non-living systems. Fifth, it synchronizes with some of the general theories of

growth and senescence as propounded by Minot, Robertson, and by ourselves (in Missouri Research Bulletins 97 and 105).

We have, tentatively, adopted equations (1) and (2) for these reasons, and because they represent the data in a most satisfactory manner.

THE MATHEMATICAL REPRESENTATION OF THE DATA

Our data are first presented for each animal separately in graphic form plotted on arithlog or semilog paper; then at the end, by way of summary, the data for all individuals of each breed and sex are plotted on the same sheet. The advantage in using arithlog paper is that a given percentage deviation from the average is represented graphically by the same distance from the average, whether the average value be large or small. This is an important consideration in charts having a very wide range in values.

Equation (2), or (1), was then fitted to the data for each individual animal; the composite charts at the end of this report are represented by the arithmetical averages of the equations of the individual animals.

Our method of fitting the equation to the data is as follows (see Missouri Research Bulletin 97 for a discussion of the advantages of the graphic method of fitting equations to this type of data): The data are plotted in such manner as to give a slope of about 45°. The best average curve is then drawn through the data points. Two weights (m_1 and m_2) were chosen on this curve, then a third weight, m_3 , such that $m_3 = \frac{1}{2}(m_1 + m_2)$. These three points being on the curve, equations could be set up to derive an expression for C in equation (2). Solving, we obtain for C ,

$$C = \frac{y_1 y_2 - y_3^2}{y_1 + y_2 - 2y_3} \quad (3)$$

in which $y = Q/m$ in equation (2).

Having computed its value from equation (3), C , is then subtracted from each of the observed values of Q/m and the differences plotted on arithlog paper. If the equation fits the data, and if the value of C has been correctly computed, the distribution of the aforesaid differences on the arithlog paper should be linear. It often happens that a slightly smaller or larger value of C improves the linearity of the distribution of the data. A and k are then computed in the usual manner as described in Missouri Research Bulletin 97.

Fig. 2 is a typical chart. It represents a steer measured practically from birth until 42 months, and grown during this interval to over 800 kilos.

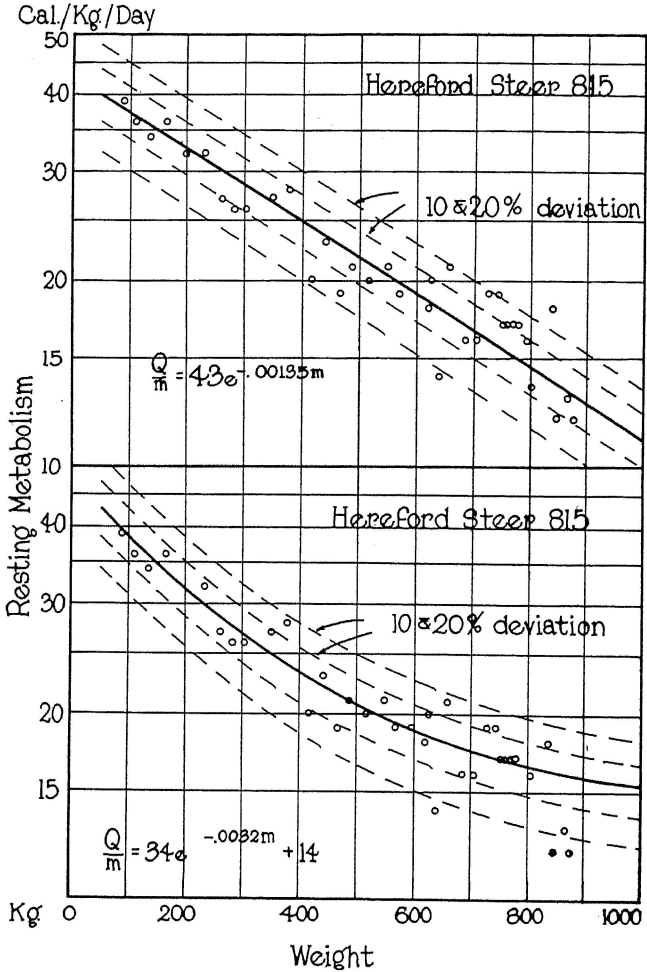


Fig. 2.—The weight changes in the *resting* metabolism during growth in a beef steer. The animal gained over 800 kilograms during the period under observation. The upper chart represents the fit of equation (1) to the data and indicates that the metabolism per unit weight decreases at 0.135 per cent of itself for every increase in one kilogram of body weight. The lower chart indicates that *theoretically* the resting metabolism per unit weight does not fall below 14 Calories per kilogram. The last three values are below the average possibly because the measurements were made by a somewhat different method, and possibly because the animal has declined somewhat in his appetite.

The upper curve represents the fit of equation (1) to the data. The observed values come within $\pm 20\%$ of the average, which is not bad considering the enormous range in weight and age covered, the great variations in environmental temperature, variations in the nature and

amount of feed consumed (he is allowed to eat all he wants, being kept in a high state of flesh known as "show condition"), and the fact that his metabolism was measured by different persons at different times, and with different apparatus of different sizes.

The representation of the data is bettered somewhat by using equation (2), as shown in the lower chart.

The upper equation

$$Q/m = 43^{-.00135m}$$

indicates that with each unit increase in body weight, the heat production per unit weight, Q/m , declines at the rate of 0.135 per cent.

The lower equation in Fig. 2 may be interpreted in a similar manner. But it also shows that the heat production never falls below 14 Calories per kilogram. Since this particular animal will probably never exceed 1000 kilos in weight, therefore it will not be possible to prove experimentally the theoretical assumption that the resting metabolism *never* declines below 14 Calories per kilogram; and it is only in this theoretical sense that the equation may not be entirely reasonable. Otherwise, the equation is altogether reasonable, every term having a clearly defined significance.

In most cases, lines indicating 10 and 20% deviations from the average are also given. This measure of deviation seems to us to be preferable to such a conventionally statistical measure as the *standard error of estimate*, for the following reasons: Assuming that the distribution of our data about the mean is "normal" (an assumption that can not be proved in the case of rapidly growing animals) the standard error of estimate, S , would indicate that 68% of all measurements fall within the limits $\pm S$. But the value S represents a large percentage for small values of the curve and a small percentage for large values of the curve, and as our interest is obviously in *percentage* deviations from the mean, therefore it seems to us that the 10 and 20% deviation lines as given in our charts are more rational in so far as they give the distribution of the data points (which may be represented in terms of percentage of all data points) within constant *percentage* deviations from the average rather than constant absolute deviation (S) from the average.

THE DATA AND THEIR INTERPRETATION

We have already discussed the data of beef animal 815, and charted his metabolism in Fig. 2.

Figures 3a to 3e represent the data for dairy cattle in graphic form. Either equation (1), or (2), or both, were fitted to the data of each animal. In case both equations were fitted to the same data, then equation

(1) is represented by a broken line, while equation (2) is represented by a continuous curve.

The data preceding pregnancy are shown by light circles; those during gestation and lactation by special symbols as indicated on the charts.

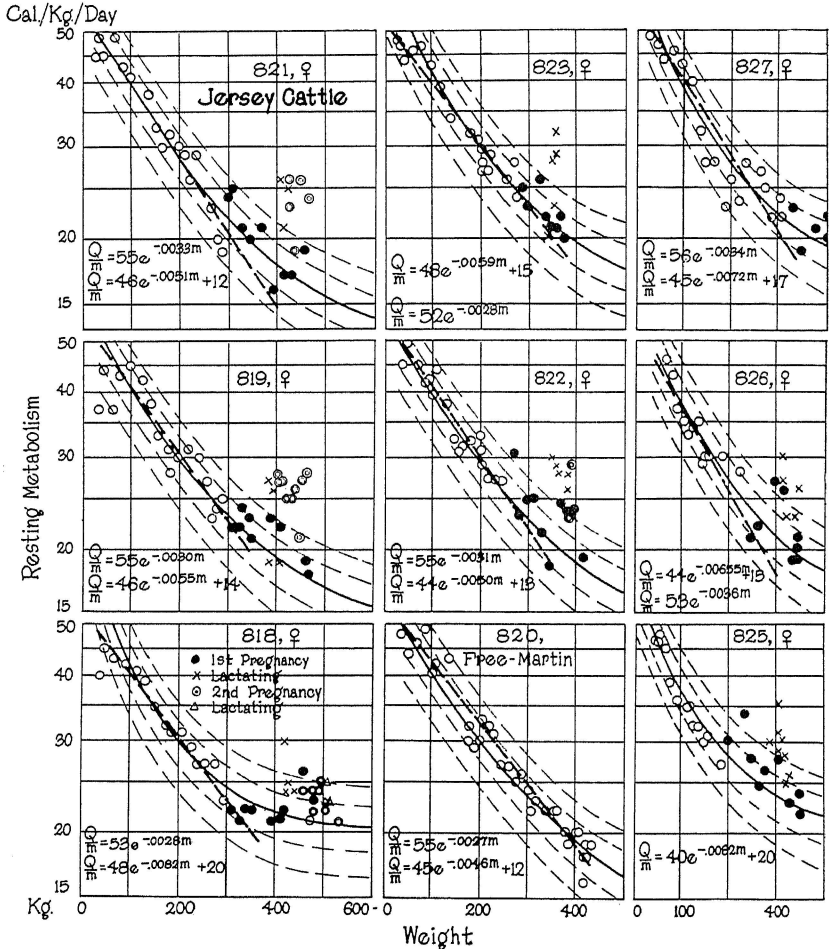


Fig. 3a.—Resting metabolism of dairy cattle (Jersey females). The broken lines represent equation (1) in the text; the solid curves represent equation (2). The light circles represent the period preceding pregnancy; the solid black circles represent the metabolism values during the first gestation; the x's represent the first lactation period; the double circles, the second gestation period; and the triangles represent the second lactation period. The high metabolism values during gestation and lactation were not considered in fitting the equation to the data.

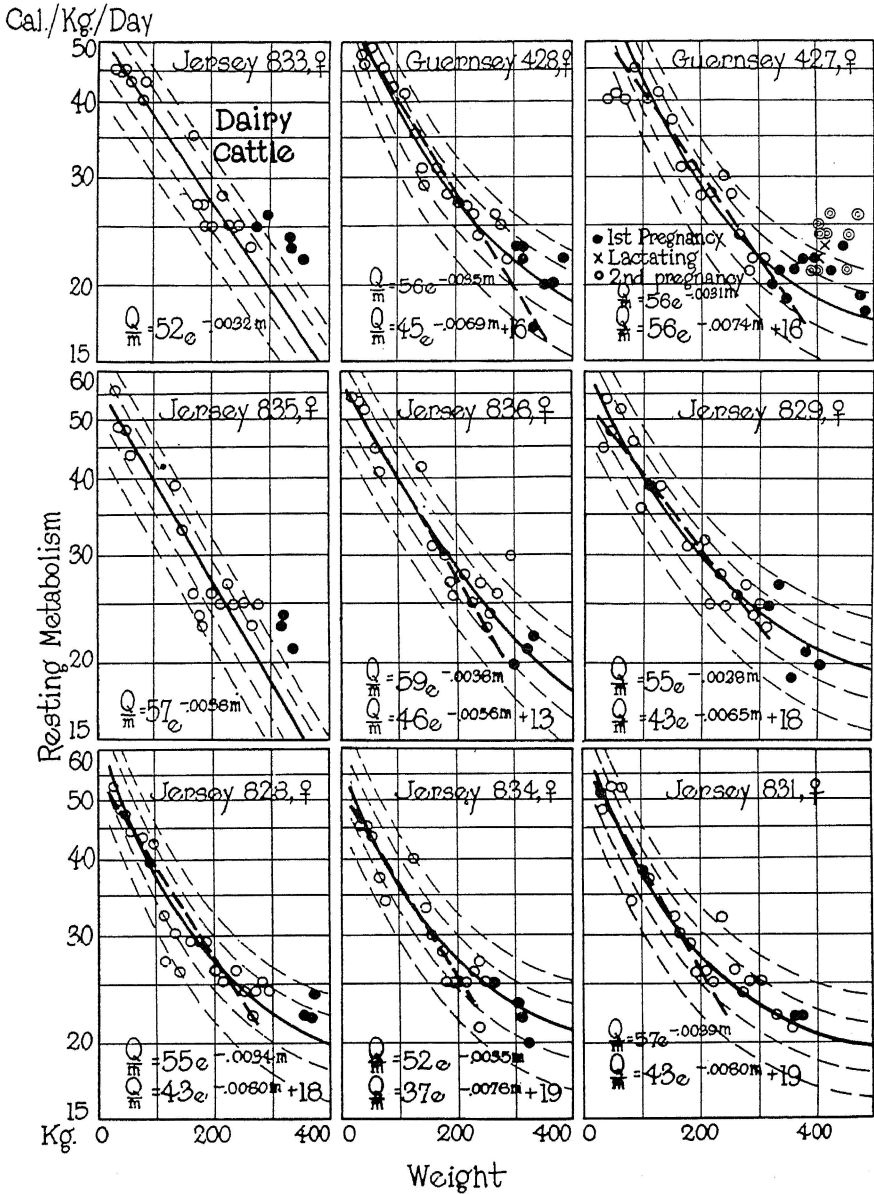


Fig. 3b.—Resting metabolism of Jersey and Guernsey females continued.

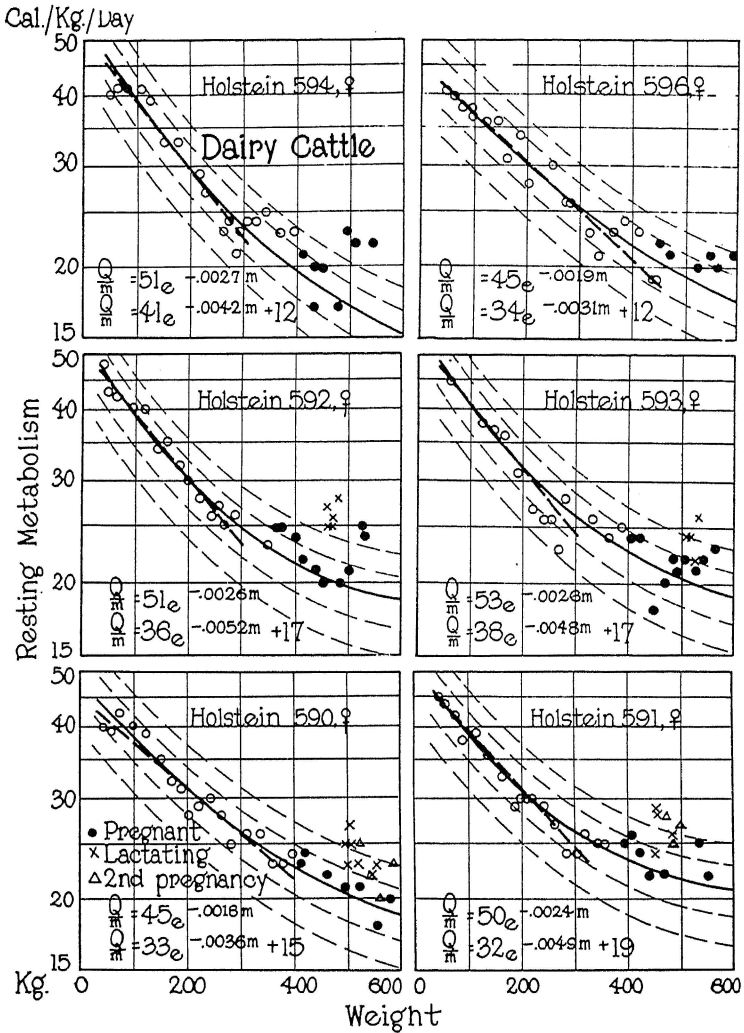


Fig. 3c.—Metabolism of Dairy cattle, Holstein-Friesian females.

The gestation metabolism data are, of course, above the average curve. The lactation metabolism data are still higher for four possible reasons. First, lactation may in itself involve a considerable energy expense; second, in the case of the dairy cattle, the animals are fed during the lactation period three (instead of two) times a day as is the practice before lactation begins, so that the interval between the feeding and measuring is shorter; third, the feed fed during lactation has a higher

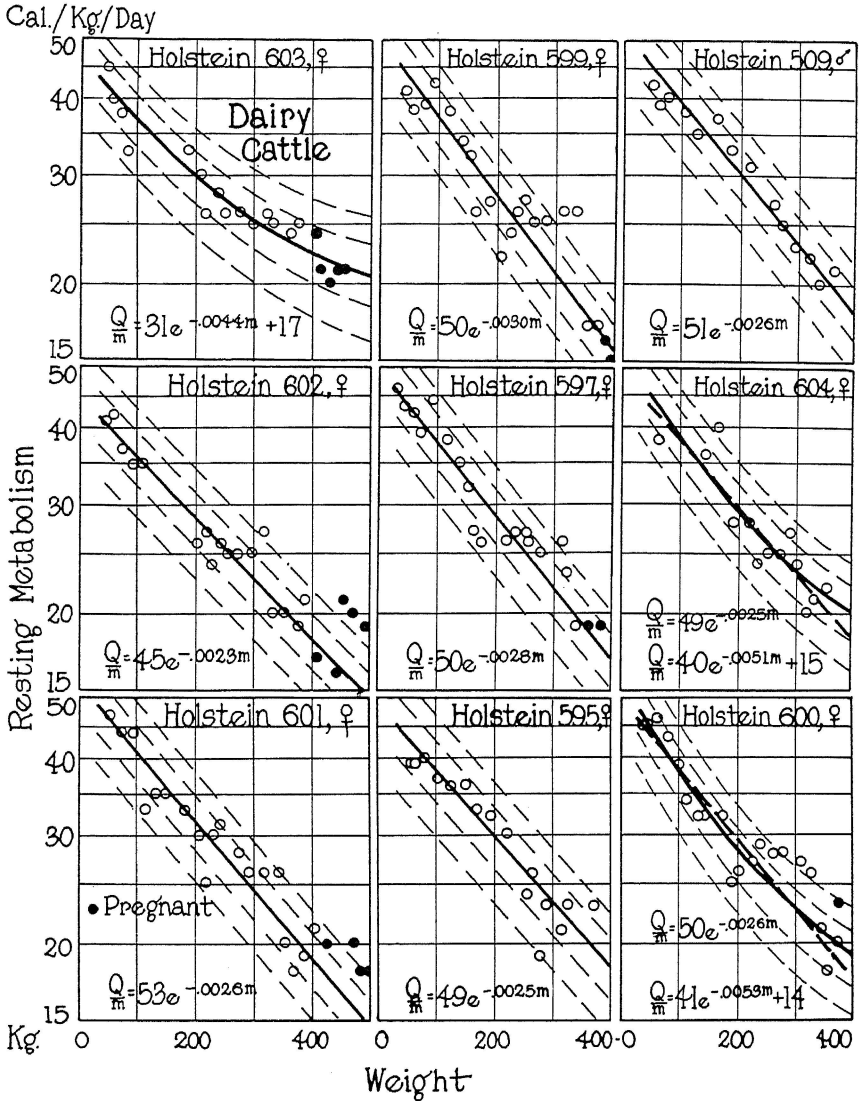


Fig. 3d.—Resting metabolism of Holstein-Friesian females continued. Females with the one exception in the upper right corner.

protein percentage so that the heat increment may be higher on this account. Fourth, the lactating animals are usually also gestating during the latter part of their lactation period. In a coming paper, we shall report some data throwing more light on these complicated questions.

Attention may be called again to the fact that up to body weight of about 300 kilograms, covering a period of very active growth, equation (1) represents the data almost as well as equation (2). But following this weight, equation (2) represents the data much more satisfactorily.

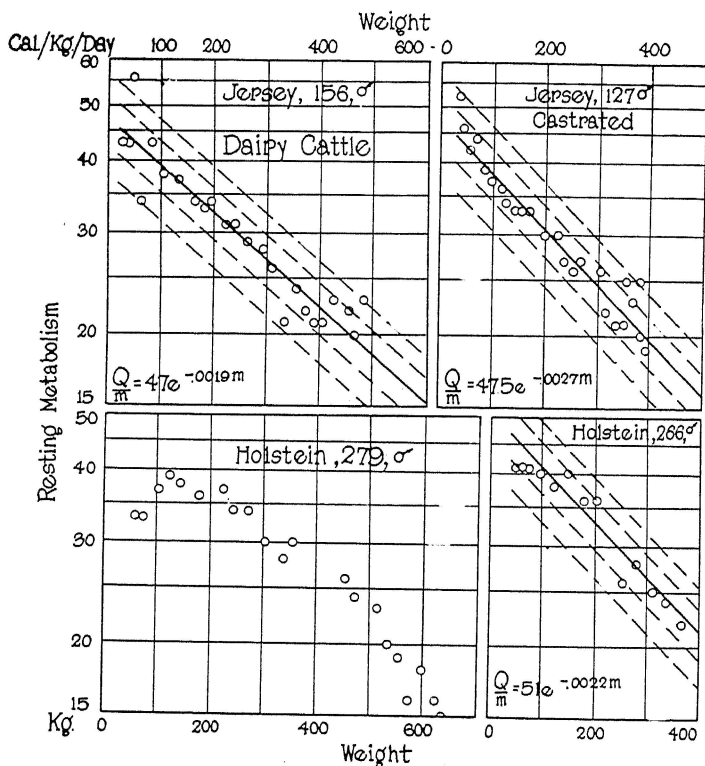


Fig. 3.—Resting metabolism of Holstein and Jersey males, and one Jersey steer (127). Note that the metabolism of the steer 127 is of the same order, and it follows the same course as the metabolism in the normal males. The changes in metabolism of Holstein male 279 follows a different course from that noticed for other animals. He is an unusually large and clumsy animal for his age. His unusual rapidity of growth and the fact that he has only one testicle are his only distinguishing characteristics.

In this connection, it is interesting to note that the free-martin 820, and the castrated animals, can be represented by equation (1) more satisfactorily than the sexed animals. However, in view of the many exceptions it is hardly appropriate to make generalizations in this respect at this time.

Similar charts are presented for the metabolism of beef cattle (Fig. 4), sheep (Fig. 5), horses (Fig. 6), and swine (Figs. 7a and 7b).

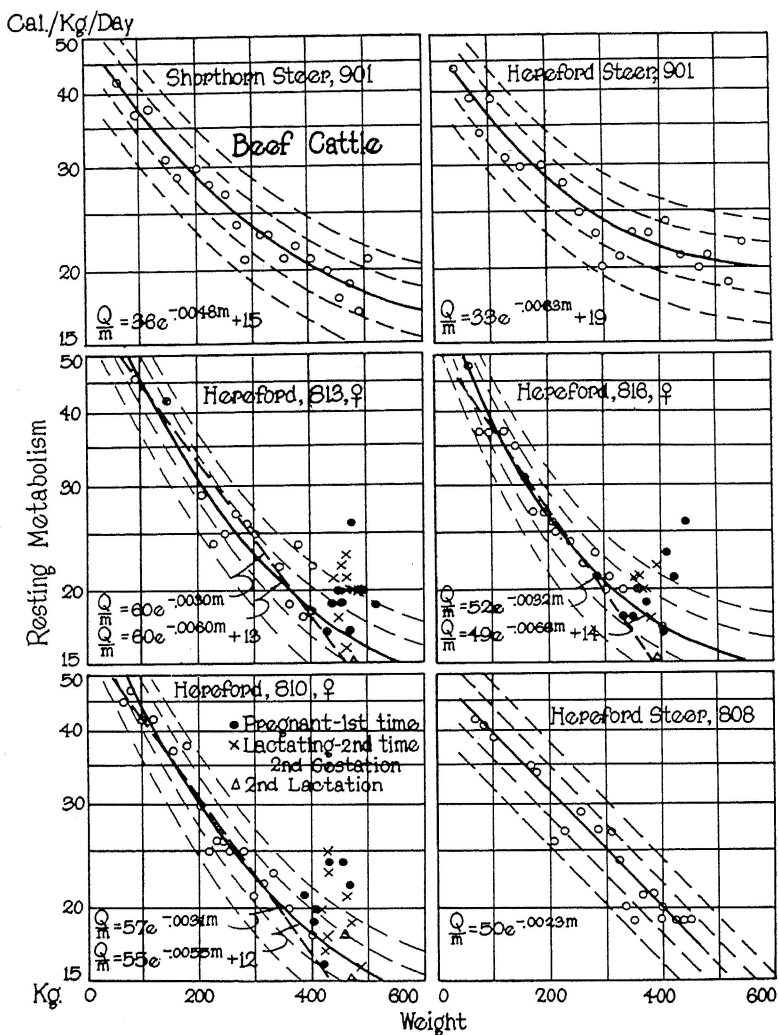


Fig. 4.—Resting metabolism of beef cattle, Hereford and Shorthorn breeds, females and castrated males. See also Fig. 2, which represents a beef steer.

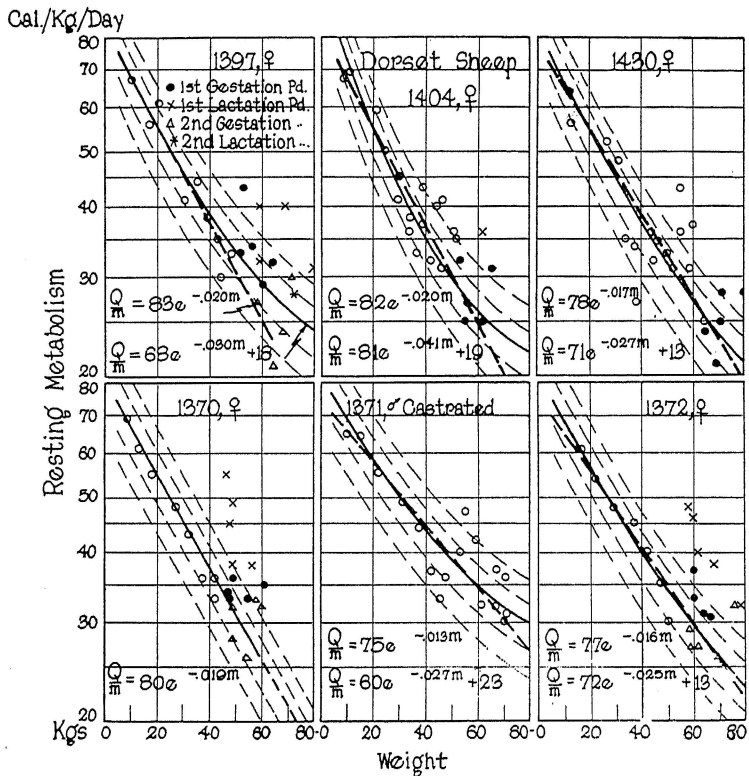


Fig. 5.—Resting energy metabolism of Dorset Sheep. The influence of lactation in sheep is as striking as in cattle.

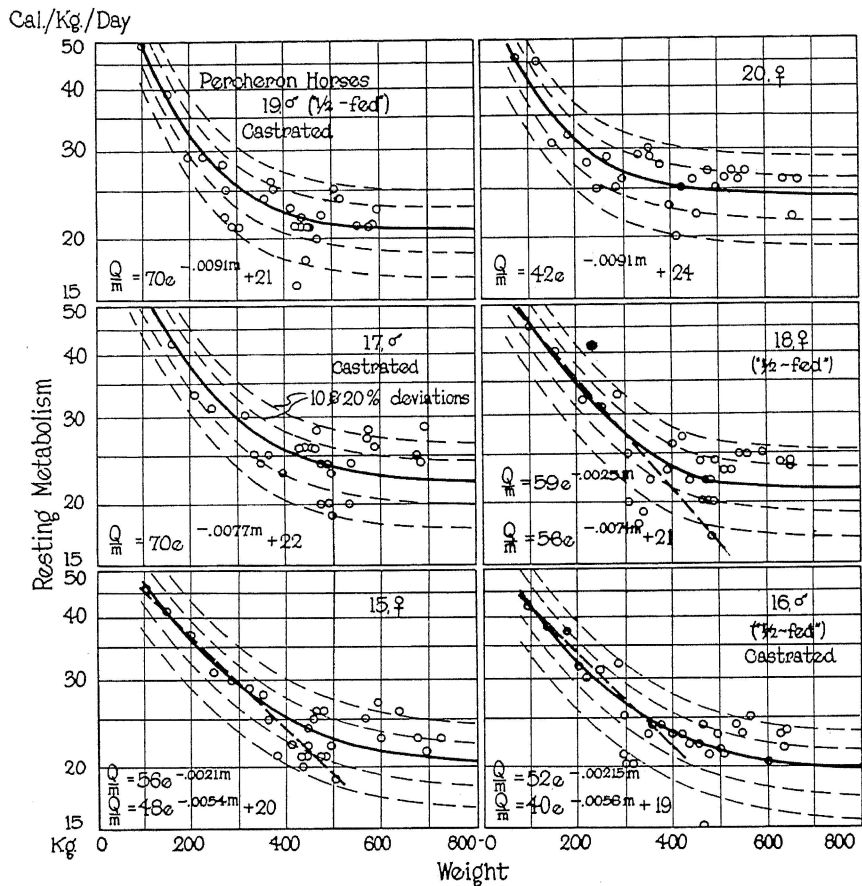


Fig. 6.—Resting metabolism of horses, Percheron females and castrated males. See Table 4 for details of feeding.

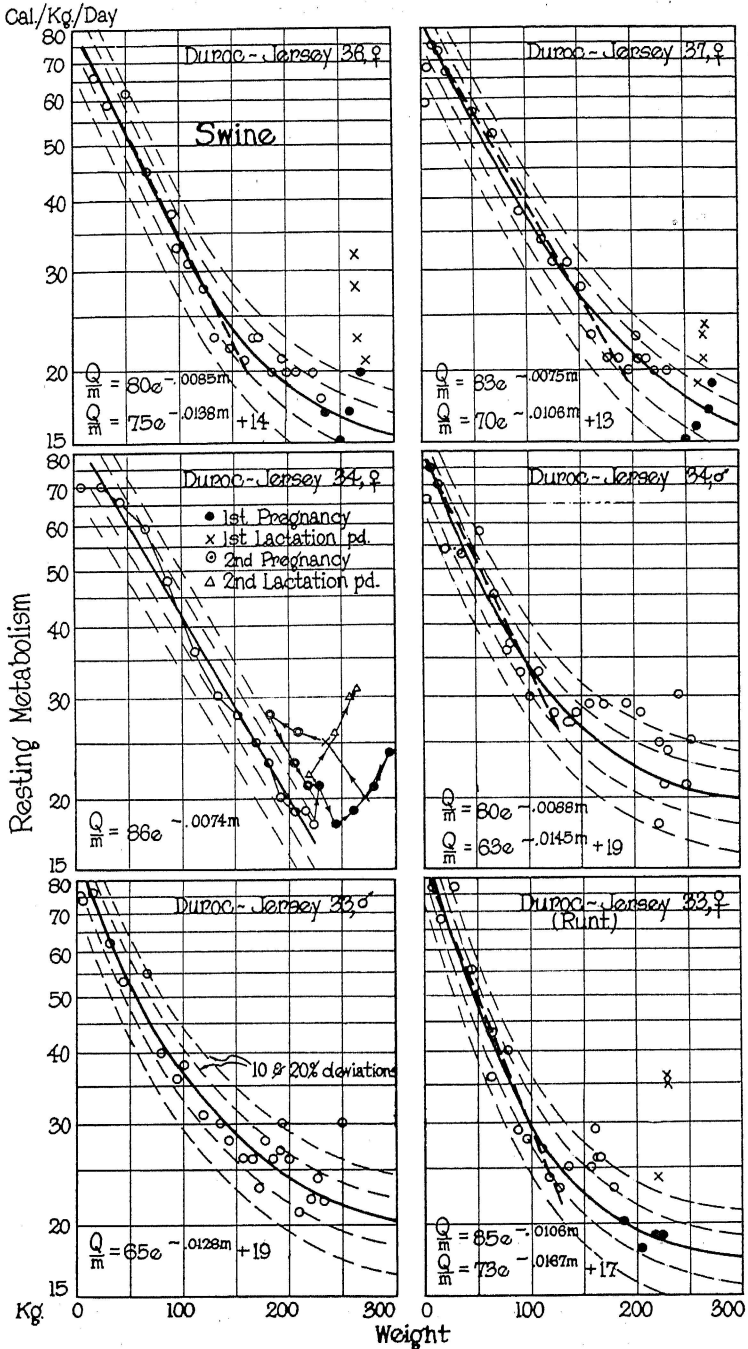


Fig. 7a.—Resting metabolism of swine, females and males of the Duroc-Jersey breed. For explanation see legend for Fig. 3a. During the lactation period, the animals were fed a milk and corn mixture, and the metabolism was measured 12 hours after feeding. Yet the metabolism values during lactation are extraordinarily high.

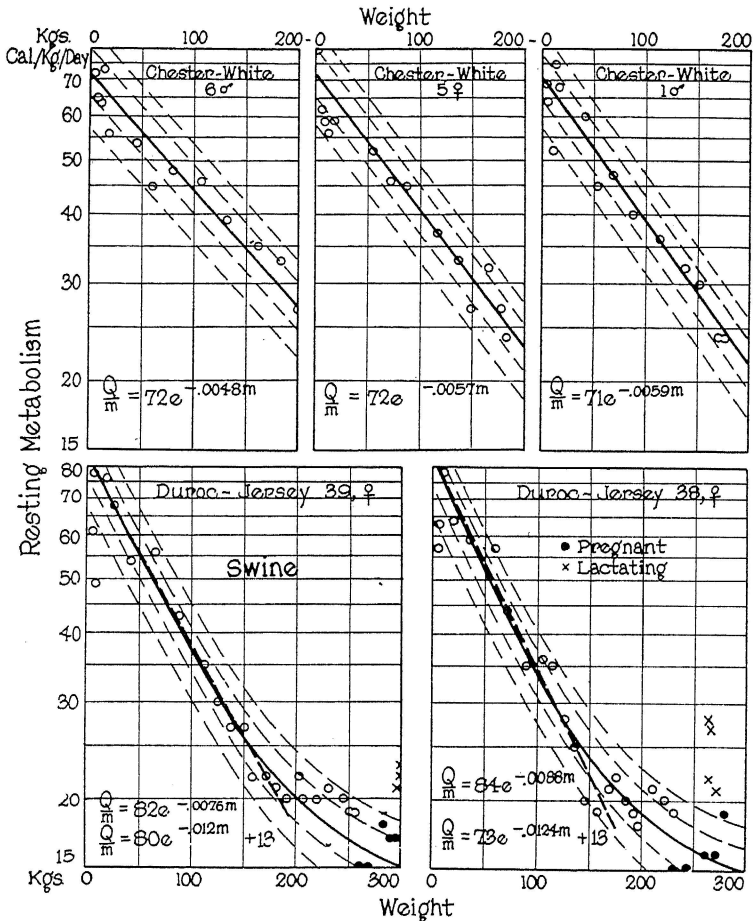


Fig. 7b.—Resting metabolism of swine, females and males of the Chester White and Duroc Jersey breeds.

The preceding curves represent the data of individual animals. There is no doubt but that the distribution of the data points about the average line is quite satisfactory considering that the measurements were not obtained under basal, or indeed under strictly reproducible, conditions.

What would be the distribution of the data points about the average if the data of *all* animals comprising the given group were plotted on the *same* charts?

Figs. 8a and 8b present such composite charts.

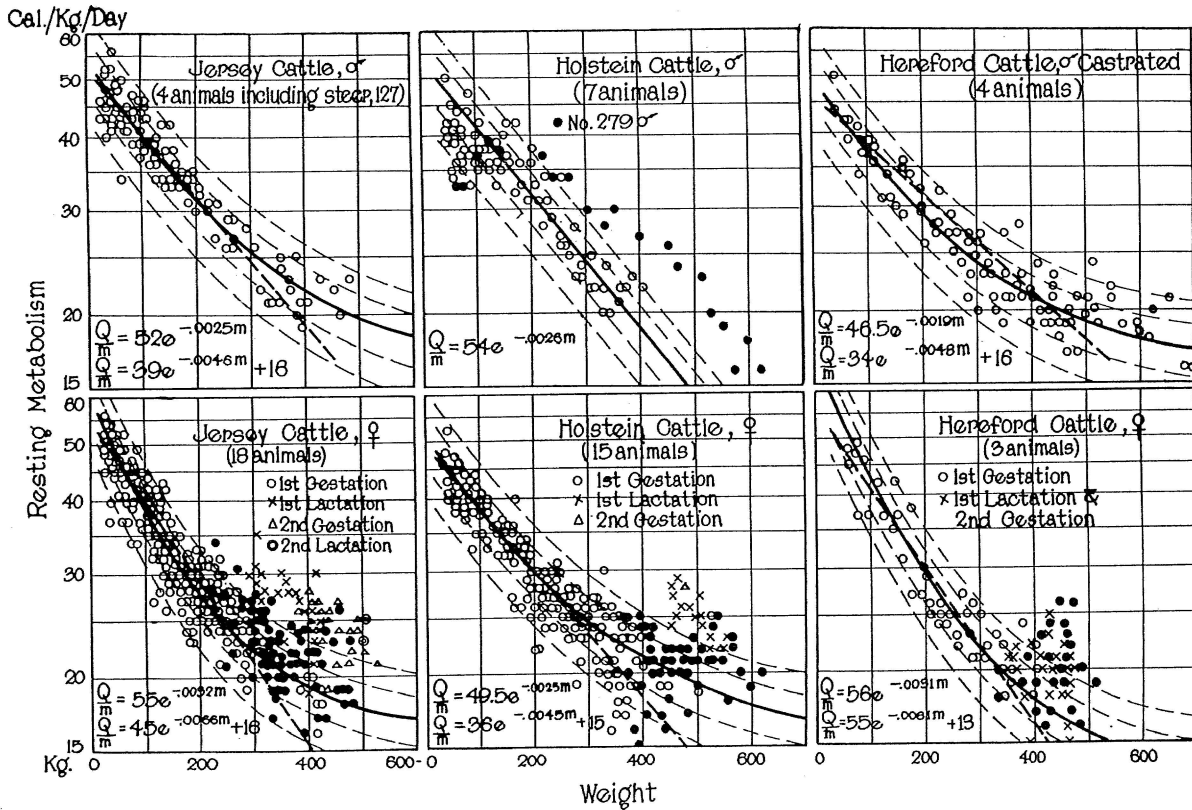


Fig. 8a.—The average resting metabolism of dairy and beef cattle. The data of the individual animals of the given sex and breed are plotted together on the same chart, and represented by equations the constants of which are arithmetical averages of the constants of the equations of the individual animals.

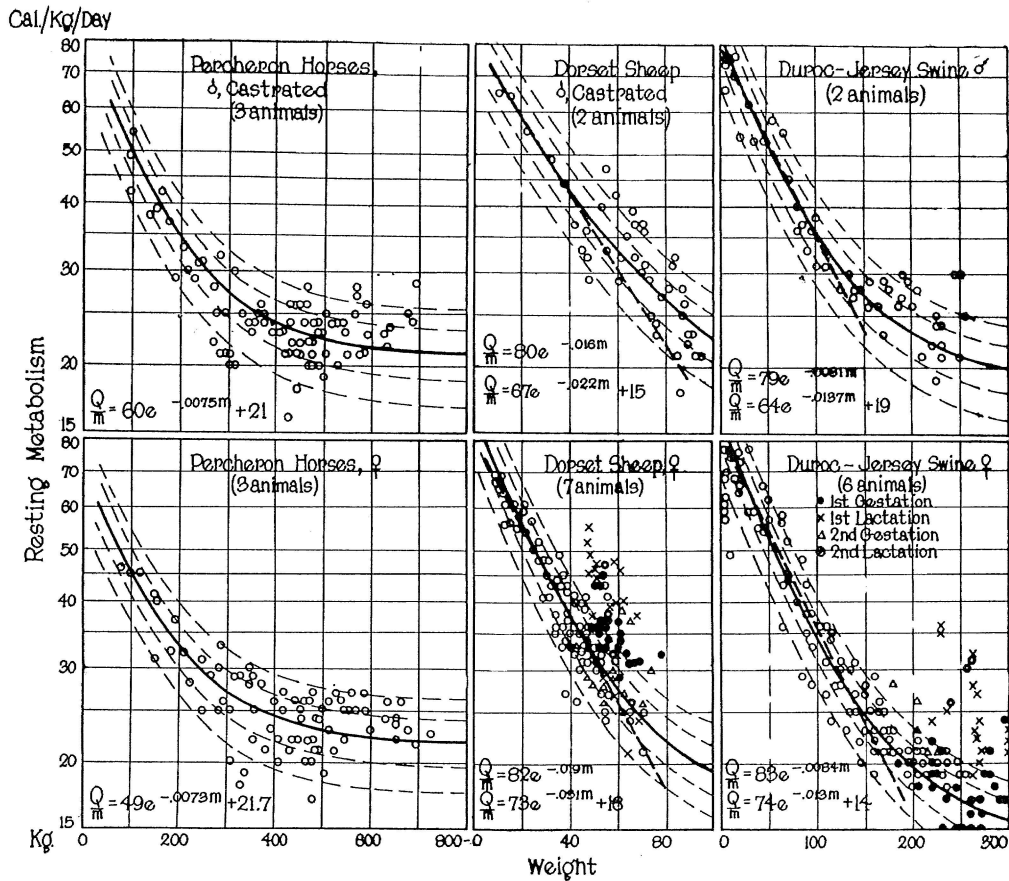


Fig. 8b.—The average resting metabolism of all horses, sheep, and swine plotted in the same manner as the data for cattle in Fig. 8a.

Fig. 8a presents the data for cattle. The Jersey male data (upper left quadrant) fall within the limits of ± 10 per cent. The Jersey female data (18 animals) fall within ± 20 per cent, except the metabolism data during lactation which as previously pointed out are far above the general metabolic level. The data for 6 of the 7 Holstein males (upper quadrant in the middle) fall within ± 10 per cent. Bull calf 279, however, is far above the level of the other animals. He is the most docile male we have; so his high metabolic level is obviously not due to restlessness. The distinguishing characteristic of this animal is his very rapid rate of growth. For any given age, he is always much heavier than his brothers; so that for any given weight on the chart, calf 279 is always younger than his brothers. Is, then, physiological age, or rapidity of growth, a factor determining metabolic rate? The Holstein female data come within ± 20 per cent of the average line—and, of course, by far the great majority of the data points fall within ± 10 per cent. The beef steer as well as the beef cow data are within the ± 20 per cent limits, with the great majority of the data points within the 10 per cent limits.

The average curves in these charts represent the arithmetical averages of the equations of the respective individuals included in the given groups. That is, the constants of the equations of the individual animals were simply averaged, and the equations in Fig. 8a represent these averages.

Fig. 8b represents, in the same manner, the horse, sheep, and swine groups of data. The distributions of the data about the average curves are the same in this chart as in Fig. 8a, and so do not call for further comment.

The wider distributions of the data points about the averages in Figs. 8a and 8b than in Figs. 2 to 7 inclusive are, of course, due to the fact that individual animals even of the same breed and sex differ somewhat in their metabolism. This is easily seen by noting differences in the numerical values of the constants of the equations of different animals (for easy comparison of constants see Table 4).

To bring out individual differences in graphic form, the curves of the equations of individual animals were plotted on the same chart in Figs. 9a and 9b.

Fig. 9a shows the curves of equation (1) of different individuals plotted on the same chart. From this, one may see that the range of individual metabolism differences is of the same order as that shown in Figs. 8a and 8b. Fig. 9b illustrates a similar situation as regards the individual curves of equation (2) in the text.

It is not easy to interpret the significance of individual variations in the rate of *resting* metabolism. They may be due to differences in

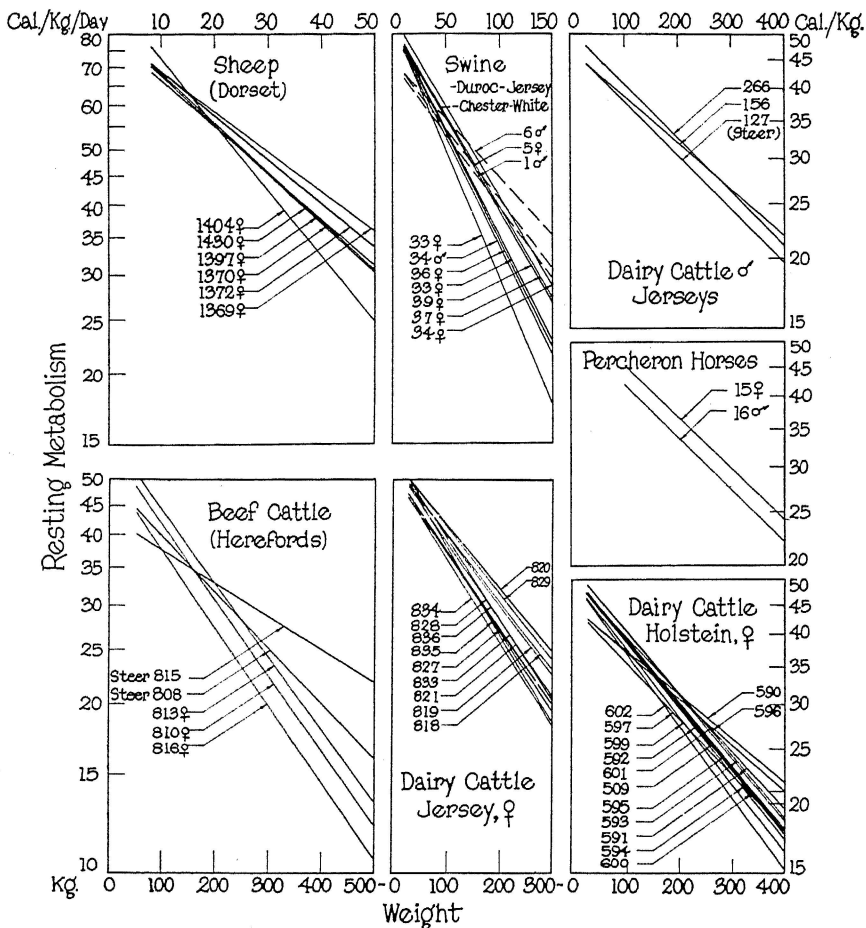


Fig. 9a.—A comparison of the individual fitted theoretical curves of equation (1), i. e., $Q/m = Ae^{-km}$. The outstanding feature in the beef cattle group is the high level of metabolism of steer 815, who is kept in a very high state of flesh; and the low metabolic level of 816, a very thin animal, and in an almost emaciated condition. The thin condition of 816 is apparently hereditary, as she seems to be well, and gets all the feed she desires. Sex as such seems to have but a slight influence on resting metabolism.

feed intake. The greater the feed intake, the greater the heat increment of feeding and therefore the higher the resting metabolic level. Beef steer 815, for example, is the heaviest feeder in the beef group, and his metabolism is therefore the highest; female 816 is the lightest feeder, and her metabolic level is the lowest. Likewise, the “ $\frac{1}{2}$ -fed” horses have a lower metabolic level than the “full-fed” horses. The same might be true as regards the dairy cattle. In a future report, we hope to present

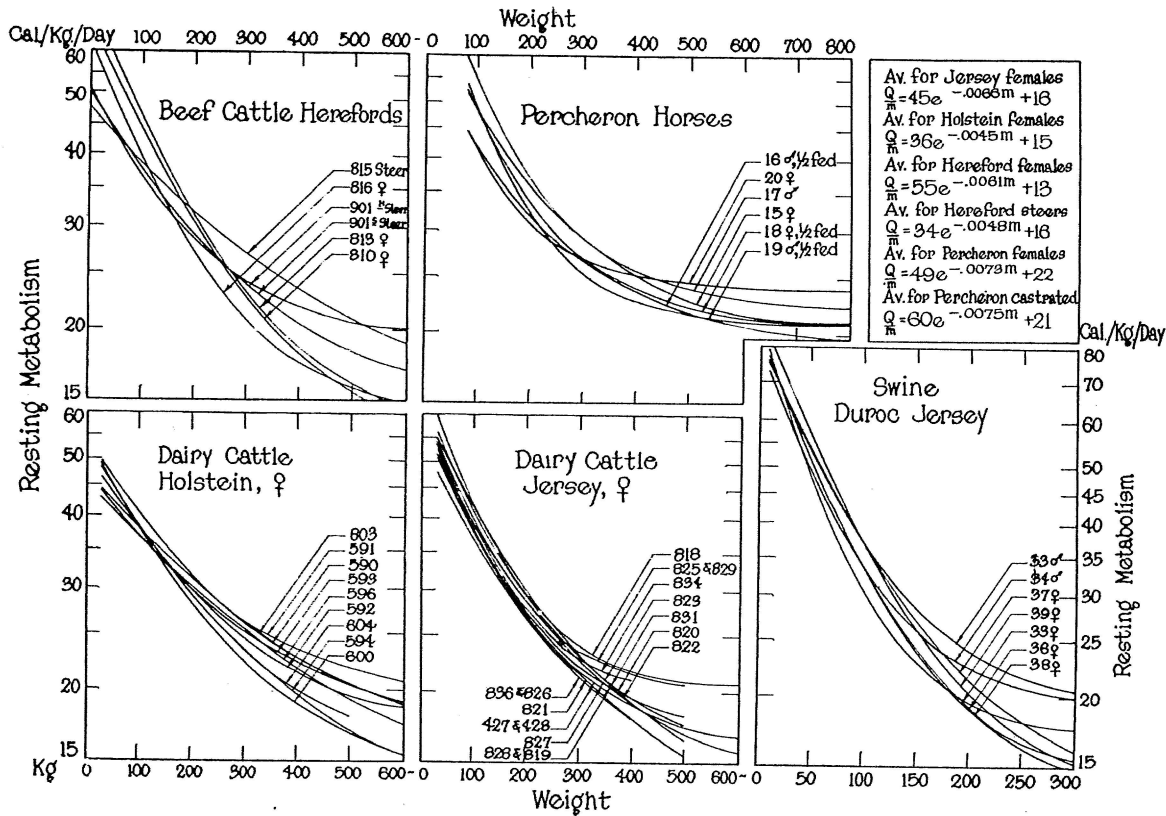


Fig. 9b.—A comparison of the individual fitted theoretical curves of equation (2), i. e., $Q/m = Ae^{-km} + C$. The remarks with regard to beef animals 815 and 816 apply here; the animals in the "1/2-fed group" of horses have a lower metabolism than the "full-fed". Dairy animal 826, the thinnest animal in the herd, also has the lowest metabolic level; but 825, equally thin, has an average metabolic level.

the relation between the feed consumption and metabolic level of individual dairy animals, which may throw some light on this problem; also, the individual *basal* metabolism data.

The suggestion has been made that there might be a functional relation between the metabolic level of an animal and its "nervous temperament" which is supposed to be a characteristic of good dairy cattle, and good race horses, and that such nervous temperament and high metabolic rate run together in families. But these are, in our present state of knowledge, only in the realm of possibilities, and there are no *a priori* reasons for assuming the presence of such relationships.

Of more immediate practical interest is the relation between the weight of an animal and its metabolic level.

It is true that the larger the animal the smaller its energy metabolism per unit weight (that is, the smaller its maintenance needs for energy per unit weight). But how rapid is the decline in metabolism with increasing weight? Does the gain of a 100 pounds by a 600-pound cow contribute as much to the energy cost of maintenance as the gain of a 100 pounds by a 1600-pound cow? This is obviously an intensely practical question, for it would ultimately enable us to determine the relation between, say, the increase in milk production with a given increase in weight of a dairy cow, and the increase in her feed consumption for maintenance for a like increase in weight; and consequently the relation between the relative efficiencies of milk (or meat) production in large and in small animals.

Mathematically, the rate of change of metabolism with increasing weight is obtained by differentiating the equation, and substituting for the desired weight.

The practical reader, however, will prefer to have a table of actual metabolic values for animals of different weights. Such values are given in Table 1 for the resting metabolism in terms of Calories per animal per day; Table 2, Calories per kilogram per day; Table 3, Calories per day for successive 50 kilo *gains* in weight.

As the resting metabolism is identical with the maintenance cost (in terms of metabolisable energy) of resting animals, then knowing the milk yield for successive increments in body weight; and knowing the maintenance cost (for energy) for the respective increments in body weight, the next step is to compare the relative efficiencies of milk production at successive levels of body weight increments and consequently the relative efficiencies of milk production in animals of different weights. We hope to report on such a computation in a future paper.

Tables 1 to 3, and Fig. 10, also show the species difference in resting metabolism (i. e., maintenance cost of resting animals in terms of me-

tabolizable energy) at different weight levels, and for successive increments in weight.

Such a comparison is not altogether satisfactory because at given weights the different species are of different birth and conception ages, and in altogether different stages of physiological development.

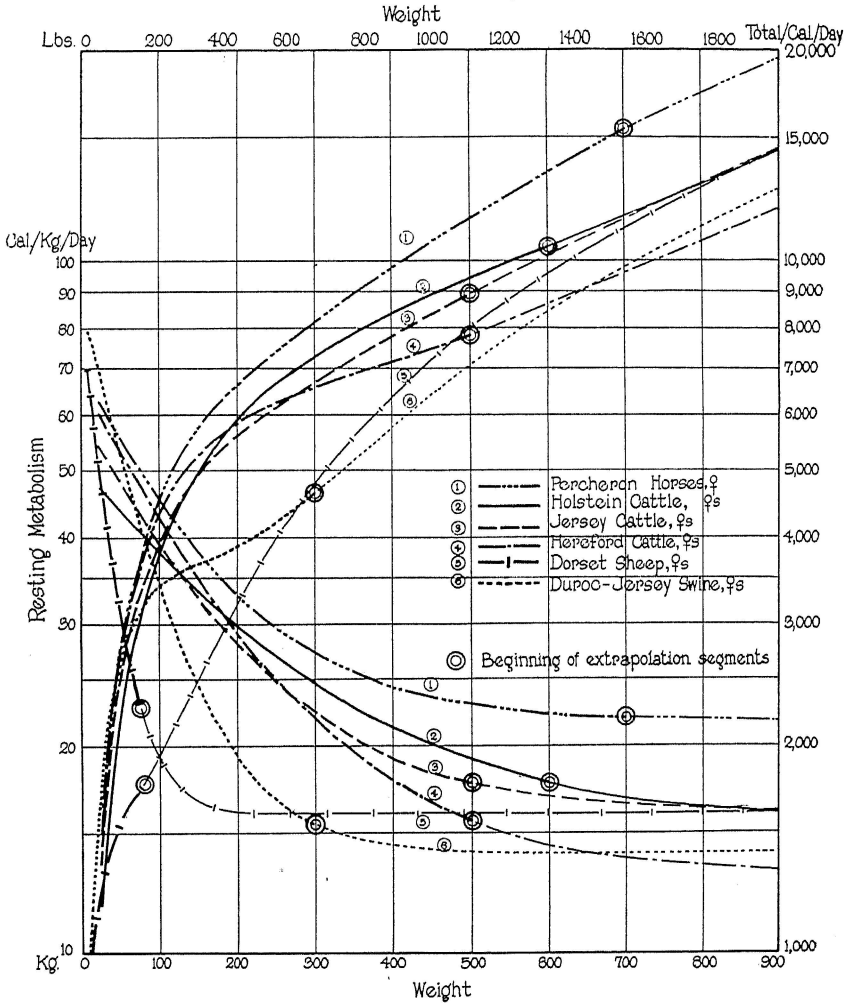


Fig. 10.—The average resting metabolism of cattle, sheep, horses and swine. The declining curves represent the metabolism per kilogram per day; the inclining curves represent the metabolism per average animal per day. The data were plotted from Tables I and II, and from the average equations given in Figs 8a and 8b. The large double circles indicate the position where extrapolation begins. Note the inflections in the curves. The exact weights at the inflections are given by the value of $2/k$ of the respective equations (see Table 3).

It is not possible to go into this question further at this time without excessive theoretical involvements; but to satisfy a possible curiosity of the readers, the resting metabolism of swine and sheep was computed to the relatively great weights that are reached by cattle and horses. These computed weights of swine and sheep, computed from equation (2) in the text, are enclosed in parenthesis in Tables 1, 2, and 3. They show that the theoretical resting metabolism is nearly the same for very great weights, and for very small weights. The significant differences between species are only as regards the rapidities with which the lowest metabolism levels per unit weight are reached. Usually, the smaller the mature weight (i. e., the more rapid its time rate of maturing), the more rapid the approach of energy metabolism per unit weight to the lowest, or mature value. Fig. 10 illustrates this idea so strikingly that no further explanations are called for.

The interpretation of the differences with which the metabolism declines with increasing weight in small animals such as sheep, and large animals such as cattle seems to be connected with the rate of growth. At a given weight either the cells of rapidly growing (i. e., immature) animals have a higher metabolism, or the process of growth calls for extra energy expense. In a future communication we shall report data on the relative metabolism of mature and immature rats of the same weight, which may throw some light on this problem.

It is probably necessary to repeat the fact that the curves of the sheep and pigs have been extrapolated from their actual weights to those that cattle and horses attain; and that extrapolations beyond factual data are always extremely hazardous, and all interpretations must necessarily be considered as very tentative and of academic interest only. The highest weights to which our animals actually attained are plainly indicated in Fig. 10, and also in Tables 1 to 3.

There are a number of peculiar irregularities in the increment table (Table 3) and also in the curves of Fig. 10. The interpretations (some of which were explained on page 14 while discussing the properties of equations (1) and (2)) of these peculiarities are for the present of mathematical rather than physiological interest, and so we shall postpone their discussion until some future time when more data will become available.

TABLE 1.—RESTING METABOLISM, CALORIES PER DAY

Wt. kgs.	Holstein		Jersey		Hereford		Horses		Swine		Sheep	
	Female	Male	Female	Male	Female	Steer	Female	Gelding	Female	Male	Female	Wether
25	1175	1265	1355	1270	1505	1155	1560	1770	1680	1610	1240	1340
50	2190	2370	2420	2350	2675	2140	2785	3110	2620	2565	1575	1865
75	3050	3330	3260	3270	3585	2980	3750	4130	3130	3140	1740	2090
100	3800	4160	3900	4060	4290	3700	4530	4930	3400	3530	*(1930)	2240
125	4435	4875	4460	4750	4825	4340	5160	5560	3550	3810	(2190)	*(2410)
150	4995	5490	4905	5340	5265	4890	5715	6075	3660	4080	(2505)	(2625)
175	5495	5985	5285	5845	5580	5370	6195	6490	3760	4340	(2850)	(2870)
200	5940	6420	5600	6320	5840	5800	6620	6880	3880	4640	(3220)	(3160)
225	6320	6770	5895	6705	6050	6210	7020	7220	4005	4930	(3625)	(3490)
250	6675	7050	6150	7100	6250	6550	7400	7550	4200	5250	(4000)	(3825)
275	6985	7260	6410	7425	6410	6900	7780	7865	4400	*(5640)	(4400)	(4150)
300	7290	7410	6660	7740	6540	7230	8160	8190	4650	(6000)	(4800)	(4530)
350	7860	7630	7175	8330	6825	7805	8925	8855	*(5145)	(6825)	(5600)	(5250)
400	8360	7640	7680	8880	7120	8400	9720	9600	(5760)	(7720)	(6400)	(6000)
450	8910		8235	9405	7425	8955	10575	10350	(6390)	(8595)	(7200)	(6750)
500	9450		8850	9950	7800	9550	11500	11200	(7050)	(9550)	(8000)	(7500)
550	9900		*(9460)	(10505)	(8195)	10120	12430	12100	(7755)	(10505)	(8800)	(8250)
600	10440		(10140)	(11100)	(8640)	10740	13380	13020	(8400)	(11400)	(9600)	(9000)
650	*(10985)		(10790)	(11700)	(9100)	11375	14365	13975	(9100)	(12350)	(10400)	(9750)
700	(11550)		(11550)	(12320)	(9660)	12040	15400	14910	(9800)	(13300)	(11200)	(10500)
750	(12150)		(12225)	(12900)	(10200)	*(12675)	(16425)	(15900)	(10500)	(14250)	(12000)	(11250)
800	(12800)		(12960)	(13600)	(10720)	(13360)	(17440)	(16880)	(11200)	(15200)	(12800)	(12000)
850	(13430)		(13770)	(14280)	(11305)	(14110)	(18530)	(17935)	(11900)	(16150)	(13600)	(12750)
900	(14040)		(14490)	(14940)	(11880)	(14760)	(19530)	(18990)	(12600)	(17100)	(14400)	(13500)

*The figures in parenthesis do not represent data; they were computed from their respective formulae and inserted for purposes of theoretical comparison only.

TABLE 2.—RESTING METABOLISM, CALORIES PER KILOGRAM PER DAY

Wt. kgs.	Holstein		Jersey		Hereford		Horses		Swine		Sheep	
	Female	Male	Female	Male	Female	Steer	Female	Gelding	Female	Male	Female	Wether
25	47.1	50.6	54.2	50.7	60.2	46.2	62.5	70.7	67.3	64.4	49.7	53.7
50	43.8	47.4	48.4	47.0	53.5	42.8	55.7	62.2	52.4	51.3	31.5	37.3
75	40.7	44.4	43.5	43.6	47.8	39.7	50.0	55.1	41.7	41.9	23.2	27.9
100	38.0	41.6	39.0	40.6	42.9	37.0	45.3	49.3	34.0	35.3	*(19.3)	22.4
125	35.5	39.0	35.7	38.0	38.6	34.7	41.3	44.5	28.4	30.5	(17.5)	*(19.3)
150	33.3	36.6	32.7	35.6	35.1	32.6	38.1	40.5	24.4	27.2	(16.7)	(17.5)
175	31.4	34.2	30.2	33.4	31.9	30.7	35.4	37.1	21.5	24.8	(16.3)	(16.4)
200	29.7	32.1	28.0	31.6	29.2	29.0	33.1	34.4	19.4	23.2	(16.1)	(15.8)
225	28.1	30.1	26.2	29.8	26.9	27.6	31.2	32.1	17.8	21.9	(16.1)	(15.5)
250	26.7	28.2	24.6	28.4	25.0	26.2	29.6	30.2	16.8	21.0	(16.0)	(15.3)
275	25.4	26.4	23.3	27.0	23.3	25.1	28.3	28.6	16.0	*(20.5)	(16.0)	(15.1)
300	24.3	24.7	22.2	25.8	21.8	24.1	27.2	27.3	15.5	(20.0)	(16.0)	(15.1)
350	22.5	21.8	20.5	23.8	19.5	22.3	25.5	25.3	*(14.7)	(19.5)	(16.0)	(15.0)
400	20.9	19.1	19.2	22.2	17.8	21.0	24.3	24.0	(14.4)	(19.3)	(16.0)	(15.0)
450	19.8		18.3	20.9	16.5	19.9	23.5	23.0	(14.2)	(19.1)	(16.0)	(15.0)
500	18.9		17.7	19.9	15.6	19.1	23.0	22.4	(14.1)	(19.1)	(16.0)	(15.0)
550	18.0		*(17.2)	(19.1)	(14.9)	18.4	22.6	22.0	(14.1)	(19.1)	(16.0)	(15.0)
600	17.4		(16.9)	(18.5)	(14.4)	17.9	22.3	21.7	(14.0)	(19.0)	(16.0)	(15.0)
650	*(16.9)		(16.6)	(18.0)	(14.0)	17.5	22.1	21.5	(14.0)	(19.0)	(16.0)	(15.0)
700	(16.5)		(16.5)	(17.6)	(13.8)	17.2	22.0	21.3	(14.0)	(19.0)	(16.0)	(15.0)
750	(16.2)		(16.3)	(17.2)	(13.6)	*(16.9)	(21.9)	(21.2)	(14.0)	(19.0)	(16.0)	(15.0)
800	(16.0)		(16.2)	(17.0)	(13.4)	(16.7)	(21.8)	(21.1)	(14.0)	(19.0)	(16.0)	(15.0)
850	(15.8)		(16.2)	(16.8)	(13.3)	(16.6)	(21.8)	(21.1)	(14.0)	(19.0)	(16.0)	(15.0)
900	(15.6)		(16.1)	(16.6)	(13.2)	(16.4)	(21.7)	(21.1)	(14.0)	(19.0)	(16.0)	(15.0)

*The figures in parenthesis do not represent data; they were computed from their respective formulae and inserted for purposes of theoretical comparison only.

TABLE 3.—RESTING METABOLISM (CAL. / DAY) INCREMENTS* FOR SUCCESSIVE 50 KILOGRAM INCREMENTS IN LIVE WEIGHTS

Wt. kgs.	Holstein		Jersey		Hereford		Horses		Wt. kgs.	Swine		Sheep	
	Female	Male	Female	Male	Female	Steer	Female	Gelding		Female	Male	Female	Wether
50	2190	2370	2420	2350	2675	2140	2785	3110	25	1680	1610	1240	1340
100	1610	1790	1480	1710	1615	1560	1745	1820	50	940	955	335	525
150	1195	1330	1005	1280	975	1190	1185	1145	75	510	575	165	225
200	945	930	695	980	575	910	905	805	100	270	390	‡(190)	150
250	735	630	550	780	410	750	780	670	125	150	280	(260)	‡(170)
300	615	360	510	640	290	680	760	640	150	110	270	(315)	(215)
350	570	220	†515	590	285	575	†165	†665	175	†100	†260	(345)	(245)
400	500	10	505	550	†295	595	795	745	200	120	300	(370)	(290)
450	†550		555	525	305	555	855	750	225	125	290	(405)	(330)
500	540		615	†545	375	†595	925	850	250	195	320	(375)	(335)
550	450		‡(610)	(555)	(395)	570	930	900	275	200	‡(390)	(400)	(325)
600	540		(680)	(595)	(445)	620	950	920	300	250	(360)	(400)	(380)
650	†(545)		(650)	(600)	(460)	635	985	955					
700	(565)		(760)	(620)	(560)	665	1035	935					
750	(600)		(675)	(580)	(540)	‡(635)	(1025)	(990)					
800	(650)		(735)	(700)	(520)	(685)	(1015)	(980)					
850	(630)		(810)	(680)	(585)	(750)	(1090)	(1055)					
900	(610)		(720)	(660)	(575)	(650)	(1000)	(1055)					
2/k †	(444)		(303)	(435)	(328)	(417)	(274)	(267)		(153)	(146)	(64.6)	(90.9)

*The metabolism increments for successive 50 kilogram weight increments were obtained from Table 1 by subtracting the metabolism values at the beginning of the given increment from metabolism at the end of the increment.

†The values 2/k represent the weight at which there is an inflection in the metabolism per day curve. The values following the first horizontal bar represent the increments following the inflection in the Q/m curve.

‡The values following the second horizontal bar, and which are enclosed in parenthesis, are not based on actual data, but were obtained from the *computed* values in Table 1. They are placed here for purposes of comparison only and show the erratic nature of the extrapolated values.

TABLE 4.—STATISTICAL DATA
 Jersey Cattle Females (Ave. Equation $Q/m = 45e^{-.0066m} + 16$)

Herd No.	Birth Date	Birth Wt. kg.	First Breeding	First Parturition	Second Breeding	Second Parturition	Constants for Equation (1)		Constants for Equation (2)			Notes
							A	100k	A	100k	C	
818	9/26/28	30.8	1/17/30	10/20/30	3/13/31	11/14/31	53	.28	48	.82	20	First calf born dead; second premature.
819	11/ 8/28	28.1	4/22/30	1/28/31	6/21/31	-----	55	.30	46	.55	14	
820	11/13/28	22.3	Free-Martin	Calf	-----	-----	55	.27	45	.46	12	
821	1/ 1/29	25.0	7/15/30	4/22/31	9/24/31	-----	55	.33	46	.51	12	
822	4/21/29	29.0	10/ 5/30	7/11/31	1/ 1/32	-----	55	.31	44	.50	13	
823	6/ 3/29	23.1	1/ 8/31	10/ 2/31	3/ 8/32	-----	52	.28	48	.59	15	"full-fed"
825	7/ 1/29	----	10/11/30	7/16/31	-----	-----	53	----	40	.82	20	"½-fed"
826	7/16/29	----	12/18/30	9/18/31	-----	-----	53	.36	44	.655	15	"½-fed"
827	11/14/29	21.8	7/22/31	-----	-----	-----	56	.34	45	.72	17	Full sister to 821.
828	12/13/29	26.3	10/17/31	-----	-----	-----	55	.34	43	.80	18	
829	12/29/29	31.8	8/28/31	-----	-----	-----	55	.28	43	.65	18	
831	2/ 1/30	26.3	12/ 2/31	-----	-----	-----	57	.39	43	.80	19	
833	2/27/30	28.7	9/ 5/31	-----	-----	-----	52	.32	-----	-----	-----	
834	2/ 9/30	29.5	10/22/31	-----	-----	-----	52	.35	37	.76	19	
835	4/ 3/30	23.8	11/19/31	-----	-----	-----	57	.38	-----	-----	-----	
836	4/ 3/30	26.3	11/ 6/31	-----	-----	-----	59	.38	46	.56	13	
427	11/ 6/28	32.7	5/14/30	-----	-----	-----	56	.31	56	.74	16	Guernsey
428	12/ 1/29	30.4	7/28/31	-----	-----	-----	56	.35	45	.69	16	Guernsey

TABLE 4.—STATISTICAL DATA (CONTINUED)
 Holstein Cattle Females (Ave. Equation $Q/m = 36e^{-.0045m} + 15$)

Herd No.	Birth Date	Birth Wt. kg.	First Breeding	First Parturition	Second Breeding	Constants for Equation (1)		Constants for Equation (2)			Notes
						A	100k	A	100k	C	
590	12/29/28	34.0	7/6/30	4/9/31	11/8/31	45	.18	33	.36	15	Sold 5/7/31.
591	2/22/29	38.3	8/22/30	5/17/31	10/14/31	50	.24	32	.49	19	
592	2/21/29	32.7	12/12/30	9/16/31	1/28/32	51	.26	36	.52	17	
593	7/30/29	----	2/4/31	11/8/31	3/8/32	53	.26	38	.48	17	
594	10/25/29	39.0	6/17/31	-----	-----	51	.27	41	.42	12	
595	11/5/29	43.7	-----	-----	-----	49	.25				
596	11/11/29	37.4	8/7/31	-----	-----	45	.19	34	.31	12	
597	11/22/29	31.8	9/11/31	-----	-----	50	.28				
599	12/16/29	37.7	9/9/31	-----	-----	50	.30				
600	1/10/30	37.9	9/16/31	-----	-----	50	.26	41	.53	14	
601	2/5/30	37.4	10/9/31	-----	-----	53	.26				
602	3/13/30	40.4	10/26/31	-----	-----	45	.23				
603	4/2/30	43.5	11/6/31	-----	-----			31	.44	17	
604	5/11/30	-----	-----	-----	-----	49	.25	40	.51	15	

Holstein Cattle Males (Equation $Q/m = 54e^{-.0026m}$)

509	8/11/29	33.8	-----	-----	-----	51	.26			
266	8/13/29	41.9	-----	-----	-----	51	.22			

Jersey Cattle Males (Equation $Q/m = 39e^{-.0016m} + 16$)

156	3/22/29	26.5	-----	-----	-----	47	.19			
127	4/26/29	30.6	-----	-----	-----	47.5	.27			Castrated 11/21/29

TABLE 4.—STATISTICAL DATA (CONTINUED)
Hereford Cattle Females (Ave. Equation $Q/m = 55e^{-.0061m} + 13$)

Herd No.	Birth Date	Birth Wt. kg.	First Breeding	First Parturition	Second Breeding	Second Parturition	Constant for Equation (1)		Constant for Equation (2)			Notes
							A	100k	A	100k	C	
810	10/10/28	-----	4/16/30	1/24/31	3/26/31	1/2/32	57	.31	55	.55	12	Weaned 8/24/29; Dried up 7/1/31; animal very fat.
813	11/12/28	-----	4/24/30	2/ 4/31	3/26/31	1/2/32	60	.30	60	.60	13	Weaned 8/24/29; Dried up 10/13/31.
816	12/19/28	-----	7/15/30	4/24/31	-----	-----	52	.32	49	.68	14	Weaned 8/24/29; Dried up 12/1/31; very thin and inferior.

Hereford & Shorthorn Cattle Steers (Ave. Equation $Q/m = 34e^{-.0018m} + 16$)

808	10 /7/28	-----	-----	-----	-----	-----	50	.23	--	-----	--	Castrated 2/1/29.
815	12/ 9/28	-----	-----	-----	-----	-----	43	.135	34	.32	14	Castrated 2/1/29; Weaned 9/6/29.
901H	2/26/20	-----	-----	-----	-----	-----	--	-----	33	.63	19	Castrated 5/1/29.
901SI	2/21/29	-----	-----	-----	-----	-----	--	-----	36	.48	15	Castrated 5/1/29.

Sheep Females (Ave. Equation $Q/m = 73e^{-.031m} + 16$)

1370	1/27/30	-----	11/18/30	4/14/31	10/17/31	3/13/32	80	1.9				
1372	1/27/30	-----	11/ 5/30	3/31/31	10/14/31	3/10/32	77	1.6	72	2.5	13	
1397	2/ 7/30	-----	1/ 1/31	4/27/31	9/21/31	2/15/32	83	2.0	68	3.0	18	
1404	2/19/30	-----	8/17/31	1/17/32	-----	-----	82	2.0	81	4.1	19	
1430	3/ 5/30	-----	10/ 7/31	3/ 2/32	-----	-----	78	1.7	71	2.7	13	

Sheep Wethers

1371	1/27/30	-----	-----	-----	-----	-----	75	1.3	60	2.7	23	Castrate 1.
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TABLE 4.—STATISTICAL DATA (CONTINUED)
Horses, Percheron Females (Ave. Equation $Q/m = 49e^{-.0073m} + 21.7$)

Herd No.	Birth Date	Birth Wt. Kg.	First Breeding	First Parturition	Second Breeding	Constant for Equation (1)		Constant for Equation (2)			Notes
						A	100k	A	100k	C	
15	3/19/29	-----	-----	-----	-----	56	.21	48	.54	20	Full-fed. Weaned 9/9/29.
18	4/22/29	-----	2/25/32	-----	-----	59	.25	56	.74	21	Half-fed. Weaned 9/9/29.
20	5/1/29	-----	2/26/32	-----	-----	---	---	42	.91	24	Full-fed. Weaned 9/9/29.
Horses, Percheron Males (Ave. Equation $Q/m = 60e^{-.0075m} + 21$)											
16	3/26/29	-----	-----	-----	-----	52	.215	40	.58	19	Half-fed. Weaned 9/9/29.
17	4/15/29	-----	-----	-----	-----	---	---	70	.77	22	Full-fed. Weaned 9/9/29.
19	4/23/29	-----	-----	-----	-----	---	---	70	.91	21	Half-fed. Weaned 9/9/29.

Note:—Preceding Feb. 1, 1930, measurements were made while animals were lying; following this date measurements were made in standing position. All were weaned September 9, 1929, when the $\frac{1}{2}$ -feeding and full-feeding began. Following January, 1930, the $\frac{1}{2}$ -fed were placed on full feed as regards hay, but continued on the $\frac{1}{2}$ -grain ration.

Swine, Duroc-Jersey Females (Ave. Eq. $Q/m = 74e^{-.0132m} + 14$)											
33	8/8/29	1.0	7/1/31	4/1	-----	85	1.06	73	1.67	17	Weaned 1/15/32.
34	8/8/29	2.9	12/17/30	4/11/31	6/22/31	86	.74	80	.85	14	Weaned 1/15/32.
36	8/8/29	2.9	7/23/31	11/15/31	-----	80	.85	75	1.38	14	Weaned 1/15/32.
37	8/8/29	2.6	7/5/31	-----	-----	83	.75	70	1.06	13	Weaned 1/15/32.
38	8/8/29	2.1	7/20/31	11/13/31	-----	84	.88	73	1.24	13	Weaned 1/13/32.
39	8/8/29	2.8	7/21/31	11/13/31	-----	82	.76	80	1.20	13	Weaned 1/15/32.
Swine, Duroc-Jersey Males (Ave. Eq. $Q/m = 64e^{-.0137m} + 19$)											
33	8/8/29	2.8	-----	-----	-----	---	---	65	1.28	19	Weaned 1/15/32.
34	8/8/29	1.6	-----	-----	-----	80	.88	63	1.45	19	Weaned 1/15/32.
Swine, Chester Whites											
1M	-----	-----	-----	-----	-----	71	.59	---	---	---	---
5F	-----	-----	-----	-----	-----	72	.57	---	---	---	---
6M	-----	-----	-----	-----	-----	72	.48	---	---	---	---

SUMMARY AND CONCLUSIONS

The two essential and original contributions in this report are: (1) Resting energy metabolism data of farm animals from birth until about three years of age; (2) mathematical analysis of the data showing a well-defined exponential relation between energy metabolism and body weight during growth.

The contribution is essential in the sense that it represents in a precise manner the changes in the general metabolic energy level with increasing weight in farm animals during growth; and that it gives definite values for metabolisable feed energy required for maintenance of resting animals of different weights during growth. It is original in the sense that no such data, or such method of relating metabolism to weight, have previously been published. The same may be said as regards the method of measuring metabolism of farm animals by the oxygen consumption method.

The *resting* metabolism data here presented differ from *basal* metabolism data in including the heat increment of feeding. Basal metabolism measured in post-absorptive condition represents Armsby's *net-energy* expended for maintenance of the resting organism; our *resting* metabolism measured at the normal non-fasting metabolic level represents *metabolisable* energy expended by the resting animal under the *given conditions* of food supply and management.

We have shown, to our own satisfaction at least, that surface area is not a reliable unit of reference for purposes of species comparisons of metabolism. For this reason and because it has not been proven that surface area is the factor limiting the metabolic rate, and because area is computed from weight anyway, it is proposed that in comparative metabolic studies metabolism should be related directly to weight, rather than to area. A simple exponential equation much used in chemistry and physics is proposed to represent this relationship. It is shown that this proposed exponential equation represents the data satisfactorily for a very wide range.

As regards species differences in metabolism of farm animals (cattle, sheep, horses, swine) the important new knowledge is this: For low weights (e. g., 25 kilos in the animals investigated) the metabolism per unit weight at a given weight is practically the same for all species. If the metabolism of the relatively small sheep and hog are extrapolated by the aid of their equations to the higher weight levels attained by cattle and horses, then we find that for large weights the metabolism per unit weight is also nearly the same for all species. The essential species differences relate to the *rapidity* with which the minimum metabolism values (per unit weight) are reached. The earlier the species

matures, the more rapidly, with respect to weight, is its limiting (minimum) metabolism attained.

The metabolism per unit weight is very high at the beginning and declines with increasing weight. A most important fact is that the *rate of decline* in metabolism per unit weight becomes less and less as the animal increases in weight; so that finally the metabolism per unit weight becomes practically constant. In other words, beyond a certain weight (or possibly age) limit the metabolism may be considered as practically proportional to weight. This seems to be a newly revealed fact: In the case of mature animals beyond a certain size, the metabolism increases directly with body weight; the metabolism per unit weight is practically constant.

Is this decline in metabolism per unit weight with increasing weight a function of the aging process, or of the mere bulk of the animal? Our animals are not only growing larger, but also growing older. Is it then age or weight that limits the metabolic rate? And what are the relative contributions of age and weight to this decline? We hope to attempt to answer this in a future communication.

The metabolism during gestation is above the general metabolic level. The metabolism during lactation is still higher. Further data are needed for the interpretation of the extraordinary high-metabolic levels during lactation.

The metabolic level is highest in the heaviest feeders, and lowest in the lightest feeders. The explanation of this fact is obvious.

The dairy cattle males have a 10 per cent higher metabolism than the females; the male hogs have a 20 per cent higher metabolism than the females, undoubtedly because the females in this species are relatively much fatter than the males.

Conditions of fatness and feeding being the same, castrated males probably have a metabolism of the same order as females; this is practically true as regards our horse data. Beef steers have a higher metabolism than females because they are usually on a higher plane of nutrition.

The slight differences in metabolism between dairy and beef cattle is probably explained by differences in feed intake and differences in fatness. Data under more comparable conditions are now being accumulated to throw light on this problem.

Horses have a higher metabolic plane than cattle of the same weight.

Sheep and swine being of a different order of mature body weight and for the same weights being in different developmental stages than cattle or horses can not be directly compared. Extrapolations of the sheep and swine data to the mature range of weights for cattle give practically the same metabolic values for all species, except horses which have a higher metabolic level.

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XVIII. Relation Between Basal Metabolism, Resting Metabolism, Heat Increments of Feeding and Body Weights in Growing Farm Mammals.*

ABSTRACT

In this paper, data are presented on *basal* metabolism of domestic animals (dairy cattle, beef cattle, sheep, horses, swine) preceding three years of age, and comparisons are made between the *basal* and the *resting* metabolism data. Basal metabolism follows the same course with increasing weight as resting metabolism (see Abstract for paper XVII). The basal metabolism values are between 25 to 30 per cent less than the resting metabolism values; this difference constitutes the heat increment of feeding. This absolute heat increment of feeding follows an exponential course with increasing body weight in the same manner as do basal and resting metabolism.

INTRODUCTION

The purposes of the immediately preceding report were: (1) Introduction to the other reports in the present series, defining the terms of, and showing the relations between, *resting* metabolism; *basal* metabolism; heat increment of feeding; metabolisable and net energy of foodstuffs; proposing an exponential law relating energy metabolism with increasing weight; showing how this law is related to the theories of Minot and Robertson on growth and senescence, and to the theories of Benedict, and Le Breton and Schaeffer concerning the relation between metabolism and "active mass". (2) Applying this law to our large body of data on *resting* metabolism during growth in farm animals.

The purpose of the present report is to extend the aforesaid exponential law to include: (1) The course of *basal* metabolism with increasing body weight in farm animals preceding the age of about three years; and (2) the heat increment of feeding during the same period (it was explained in the preceding report that the heat increment of feeding is the difference between *resting* and *basal* metabolism).

It was explained in the preceding report that the term *basal* metabolism as applied to humans may be used to represent the metabolism in farm animals, but possibly only in a figurative sense because the physiological condition of these large animals on reaching the post-absorptive condition (requiring 2 to 4 days of fasting) may be different than in humans (reaching this condition about 12 hours after feeding). Our "basal metabolism" data were obtained on animals lying in natural position and having fasted from 48 to 96 hours.

The question as to the required duration of fast for reaching post-absorptive condition in farm animals has not been definitely answered.

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The following paragraphs are intended to give the most recent findings in this field as they relate to ruminants.

In the case of sheep, Benedict and Ritzman (1931) have found that a respiratory quotient of 0.82 is reached between 26 and 47 hours after feeding. (See Table 1.) The urinary nitrogen excretion was not taken into consideration in this computation. Since a respiratory quotient of 0.82 (including the protein metabolism) is reached in humans about 12 hours after feeding when the post-absorptive condition is said to be reached, therefore the sheep 26 to 48 hours after feeding may be considered to be in the same nutritive condition as man 12 hours after a meal, and the metabolism at this time may perhaps be considered as fasting or possibly basal metabolism under comparable conditions of rest.

TABLE 1.—THE COURSE OF DECLINE OF THE RESPIRATORY QUOTIENT WITH LAPSE OF TIME AFTER FEEDING IN SHEEP. (FROM BENEDICT AND RITZMAN, 1931, P. 51.)

Hours without food	R. Q.	Hours without food	R. Q.
2	0.97	$\frac{3}{4}$	1.04
10	0.94	9	0.93
18	0.90	17	0.92
26	0.82	23	0.91
34	0.81	31	0.89
42	0.79	39	0.85
50	0.78	47	0.82
58	0.73	55	0.75
66	0.73	63	0.75
74	0.72	71	0.75
82	0.71	79	0.73
90	0.71	87	0.72

In the case of cattle (beef steers) Benedict and Ritzman (1927) found the average R. Q. to be 0.83 between 25 and 35 hours of fasting and a R. Q. of 0.75 to 0.76 between 47 and 50 hours of fasting. They summarize their findings as follows: "The respiratory quotient, when the steer was receiving feed regularly was about 1.00 or above, depending somewhat upon the character of the feed and the time elapsing after feed has been eaten. On the first day of fasting, the quotient was about 0.82 or 0.83. On the second and third days, it was still lower, but after the third day it remained fairly constant at about 0.79, indicating that the steer was burning essentially fat". Benedict and Ritzman believe that for cattle on a maintenance ration, "It would seem more logical, therefore, to employ the measurements made about the thirtieth hour after food as corresponding to the 12-hour interval without food in the base of humans".

Forbes, Braman, Kriss and associates in a very recent publication (Dec., 1931) state that in beef cattle "It seems that true fast may be

attained as early as the second day after the withdrawal of food, and that it will certainly be reached by the fourth day", and give the following values for the *non-protein* respiratory quotient at different stages of fasting. (Table 2).

TABLE 2.—VALUES FOR THE NON-PROTEIN RESPIRATORY QUOTIENT AT DIFFERENT STAGES OF FASTING. (FROM FORBES, BRAMAN, KRIS AND ASSOCIATES, 1931.)

Days of fast	Steer 85 Period 12	Steer 17 Period 7	Steer 17 Period 9	Steer 17 Period 11	Steer 17 Period 13	Steer 85 Period 10
1st	0.81	-----	-----	-----	-----	-----
2nd	0.71	(0.72)	-----	-----	0.71	-----
3rd	0.70	(0.69)	(0.73)	0.74	0.72	-----
4th	-----	(0.70)	(0.68)	0.71	0.71	0.71
5th	-----	(0.70)	(0.70)	0.71	-----	0.71
6th	-----	(0.71)	-----	-----	-----	-----

These results appear to be in agreement with the R. Q. values given by Benedict and Ritzman (1927) for cattle.

In the light of the above results we feel that the method we have followed in fasting our animals from 48 to 96 hours meets the requirements for post-absorptive condition, and our energy metabolism data here presented may be considered as "basal metabolism" as far as this term can be applied with propriety to farm animals.

BASAL METABOLISM AND AVERAGE HEAT INCREMENTS OF FEEDING IN DAIRY CATTLE

The curves representing the course of *resting* energy metabolism of dairy cattle as given in the preceding report are also shown herewith in Fig. 1 in the form of broken curves.

The data points below these broken curves represent the observed *basal* metabolic values of cattle (fasted 48 to 72 hours). The continuous curves drawn through these data points represent equation (2) presented in the immediately preceding report, fitted to these basal metabolic values. So here we have on the same charts both the *basal* and the *resting* metabolism of dairy cattle; and the same form of exponential equation is fitted to both sets of data. The curve of basal metabolism per unit weight with increasing weight is seen to follow the same course as the curve of resting metabolism.

The numerical values of the exponents are the same in the upper (resting) and the lower (basal) curves. In other words, the *percentage* differences between resting and basal metabolism are the same for all regions of the curves.

These percentage differences are given for all curves. Thus in the lower left chart the percentage differences between the resting and basal metabolism is practically 27 per cent. It means that the lower (basal) curve, is, at all points, 27 per cent less than the upper (resting) curve.

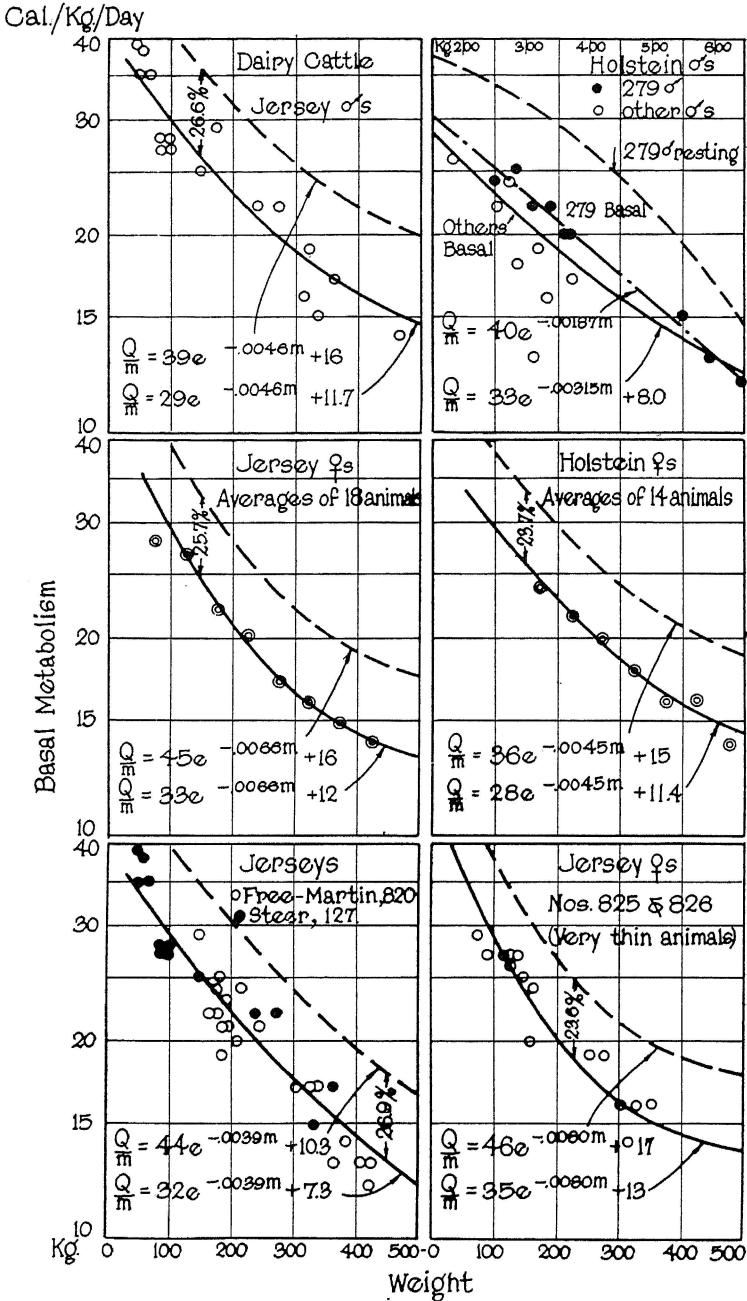


Fig. 1.—The course of change of basal metabolism with increasing weight during growth in dairy cattle. The circles represent observed values. The continuous curves drawn through the circles represent equation (1) fitted to these data. The broken curves represent the resting metabolism as copied from the charts in the preceding report of this series. The two quadrants in the middle of the chart represent our entire populations of Jersey and Holstein females (averages respectively of 18 and 14 animals). The upper quadrants represent males; the lower left quadrant represents unsexed animals; the lower right quadrant represents unusually small and emaciated animals.

Now since the upper (resting metabolism) curve represents the general and relatively constant level of metabolism of normally-fed animals with the normal "fill" in the digestive tract, while the lower (basal metabolism) curve represents the metabolism in nearly post-absorptive condition; therefore the difference represents the heat increment of feeding.

Fig. 1 shows, that in dairy cattle, under the given conditions of feeding and management (1) the heat increment of feeding is directly proportional to the resting metabolism at practically all body weights (and therefore ages); (2) the heat increment of feeding is between 24 and 27 per cent of the resting metabolism; (3) the *basal* metabolism is from 24 to 27 per cent less than the resting metabolism.

The absolute values of the heat increments at various weights are, of course, easily computed by merely multiplying the resting metabolism by the percentages given on the curve. These values for dairy cattle are given in Table 3. Knowing the feed consumption per day, these heat increments may be represented in terms of the feed consumed, or in terms of the metabolisable energy consumed. This phase of the problem will be discussed in a future report.

The two middle quadrants of Fig. 1 represent the averages of our normal females, of the Jersey and Holstein breeds. In the Jerseys, the average basal metabolism values are 26 per cent below the resting metabolism values; in the Holsteins 24 per cent.

The upper left quadrant represents individual measurements of Jersey males and the upper right quadrant, individual measurements of Holstein males. For the Jersey males the difference between resting and basal metabolism is 27 per cent. The Holstein male data are not sufficiently extensive for definite conclusions. The peculiar behaviour of the data for Holstein male 279, has been discussed in the preceding paper.

The lower left quadrant represents data for one castrated male and one free-martin female. The data points represent individual measurements. There is nothing unusual about these data.

The lower right quadrant represents two very thin and small animals. The data points represent individual measurements. The *percentage* difference between the resting and basal metabolism of these small animals is the same as of the large Holstein animals; so that the *absolute* difference between resting and basal metabolism is less for the small animals than for the large animals.

Table 3 is presented by way of a numerical summary of this section. In this Table are given by 25-kilogram intervals the resting and basal metabolism values, and the absolute heat increments of feeding.

TABLE 3.—RESTING METABOLISM, BASAL METABOLISM, AND HEAT INCREMENT OF FEEDING IN DAIRY CATTLE

Wt. Kgs.	Heat Production in Calories per Day														
	Resting Metabolism					Basal Metabolism					Heat Increment of Feeding				
	Hols. Fems.	Jersey Fems.	Under- fed Jersey Fems.	Jersey Steer & Free- Martin	Jersey Males	Hols. Fems.	Jersey Fems.	Under- fed Jersey Fems.	Jersey Steer & Free- Martin	Jersey Males	Hols. Fems.	Jersey Fems.	Under- fed Jersey Fems.	Jersey Steer & Free- Martin	Jersey Males
25	1175	1355	1368	1255	1270	897	1007	1045	917	932	278	348	323	338	338
50	2190	2420	2390	2325	2350	1671	1798	1826	1700	1725	519	622	564	625	625
75	3050	3260	3173	3233	3270	2327	2422	2424	2363	2400	723	838	749	870	870
100	3800	3900	3770	4010	4060	2899	2898	2880	2931	2980	901	1002	890	1079	1080
125	4435	4460	4238	4663	4750	3384	3314	3238	3409	3486	1051	1146	1000	1254	1264
150	4995	4905	4620	5220	5340	3811	3644	3530	3816	3920	1184	1261	1090	1404	1420
175	5495	5285	4970	5688	5845	4193	3927	3797	4158	4290	1302	1358	1173	1530	1555
200	5940	5600	5260	6100	6320	4532	4161	4019	4459	4639	1408	1439	1241	1641	1681
225	6320	5895	5535	6435	6705	4822	4380	4229	4704	4921	1498	1515	1306	1731	1784
250	6675	6150	5800	6725	7100	5093	4569	4431	4916	5211	1582	1581	1369	1809	1889
275	6985	6410	6078	6958	7425	5330	4763	4644	5086	5450	1655	1647	1434	1872	1975
300	7290	6660	6360	7170	7740	5562	4948	4859	5241	5681	1728	1712	1501	1929	2059
325	7605	6923	6630	7378	8027	5803	5144	5065	5393	5892	1802	1779	1565	1985	2135
350	7860	7175	6930	7525	8330	5997	5331	5295	5501	6114	1863	1844	1635	2024	2216
375	8138	7425	7238	7688	8588	6209	5517	5530	5620	6304	1929	1908	1708	2068	2284
400	8360	7680	7560	7800	8880	6379	5706	5776	5702	6518	1981	1974	1784	2098	2362
425	8628	7948	7863	7948	9138	6583	5905	6007	5810	6707	2045	2043	1856	2138	2431
450	8910	8235	8190	8055	9405	6801	6119	6257	5888	6903	2109	2116	1933	2167	2502
475	9120	8550	8550	8170	9690	6959	6353	6532	5972	7112	2161	2197	2018	2198	2578
500	9450	8850	8900	8250	9950	7210	6576	6800	6031	7303	2240	2274	2100	2219	2647

BASAL METABOLISM AND AVERAGE HEAT INCREMENTS OF FEEDING IN BEEF CATTLE

Fig. 2, shows the relation between *basal* and *resting* metabolism with increasing weight during growth in beef cattle in the same manner as Fig. 1 shows it for dairy cattle. The data points represent individual measurements. The distribution of the data points for beef cattle is not as satisfactory as for dairy cattle because they were not fasted as often; because fewer animals were included in the group; because the animals in the beef group are less uniform. Thus steer 815 is very fat, being kept in a show condition, and in order to keep him in this condition the management did not favor fasting him. No. 816 on the other hand is extremely thin, being a very poor feeder. Also, the steers, particularly 815, have been nursing either their dams, or foster dams, to quite an advanced age. The percentage differences between the basal and resting metabolism are indicated on the chart for each animal. On the whole, one is safe in concluding that the differences between basal and resting metabolism in beef cattle are of the same order as in dairy cattle, namely about 25 per cent.

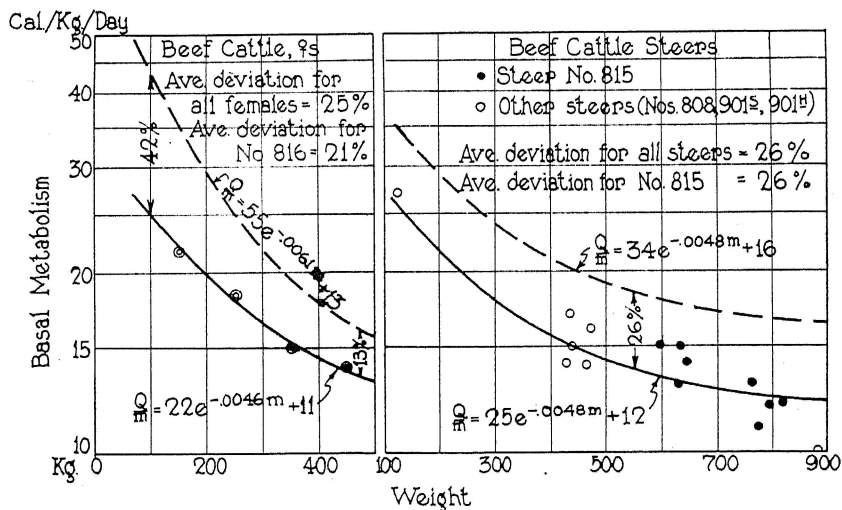


Fig. 2.—The course of change of *basal* metabolism with increasing weight of beef cattle. The circles represent individual observed values. The broken curves represent *resting* metabolism. The smooth curves represent the *basal* metabolism. The equations of these curves are given in the chart.

Table 4 presents the numerical summary for resting metabolism, basal metabolism, and heat increment of feeding for beef cattle in the same manner as Table 3 presents it for dairy cattle.

TABLE 4.—RESTING METABOLISM, BASAL METABOLISM, AND HEAT INCREMENT OF FEEDING IN BEEF CATTLE

Weight Kgs.	Heat Production in Calories per Day					
	Resting Metabolism		Basal Metabolism		Heat Increment of Feeding	
	Females	Steers	Females	Steers	Females	Steers
25	1505	1155	765	855	740	300
50	2675	2140	1420	1584	1255	556
75	3585	2980	1995	2205	1590	775
100	4290	3700	2480	2738	1810	962
125	4825	4340	2913	3212	1912	1128
150	5265	4890	3300	3619	1965	1271
175	5580	5370	3640	3974	1940	1396
200	5840	5800	3940	4292	1900	1508
225	6050	6210	4230	4595	1820	1615
250	6250	6550	4475	4847	1775	1703
275	6410	6900	4730	5106	1680	1794
300	6540	7230	4950	5350	1590	1880
325	6695	7508	5168	5556	1527	1952
350	6825	7805	5390	5776	1435	2029
375	6975	8100	5588	5994	1387	2106
400	7120	8400	5800	6216	1320	2184
425	7268	8670	5993	6416	1275	2254
450	7425	8955	6165	6627	1260	2328
475	7600	9263	6365	6855	1235	2408
500	7800	9550	6600	7067	1200	2483
525	----	9818	----	7265	----	2553
550	----	10120	----	7489	----	2631
575	----	10408	----	7702	----	2706
600	----	10740	----	7948	----	2792
625	----	11063	----	8187	----	2876
650	----	11375	----	8417	----	2958
675	----	11678	----	8642	----	3036
700	----	12040	----	8910	----	3130

Fig. 3 represents a comparative graphic summary of the basal metabolism of dairy and beef breeds of our own animals (continuous curves copied from figures 1 and 2), and the fasting metabolism data for beef steers of Benedict and Ritzman (light circles), and of Forbes, Braman, Kriss and associates (dark circles). The data by Benedict and Ritzman are taken from pp. 166-9, Publication 377 (1927) of the Carnegie Institution of Washington, while the data by Forbes and associates were kindly sent to us by Director Forbes and Professor Kriss of the Pennsylvania Institute of Animal Nutrition, their tables being reproduced herewith (Table 5).

The data by Benedict and Ritzman (represented in Fig. 3 by light circles) represent metabolism values between 49 and 55 hours after feeding.

TABLE 5.—FASTING METABOLISM DATA FOR BEEF STEERS SENT TO US BY DIRECTOR FORBES AND PROFESSOR KRISS OF THE PENNSYLVANIA STATE COLLEGE INSTITUTE OF ANIMAL NUTRITION (1932)

Experiment, Animal and Period No.	Date of Measurement	Breed	Age	Wt.	Fasting Metabolism per day		Time after feeding	Level of feeding prior to fast	Publication reference
					Per head	Per kg. live wt.			
Exp. 241			<i>Months</i>	<i>Kg.</i>	<i>Cals.</i>	<i>Cals.</i>	<i>Days</i>		
Steer 17	1929	Shorthorn							
Period 7	Jan. 1-2		17	324	6011	18.55	3	Maintenance	Jour. Agr. Research Vol. 43, No. 11 pp. 1003-1014 (1931)
Period 9	Jan. 30-31		18	322	6108	18.94	4	"	
Period 11	March 14-15	20	338	6375	18.87	4	"		
Steer 85		Shorthorn							
Period 10	April 2-3		21	340	6611	19.45	3	"	
Period 12	May 14-15		22	348	6752	19.41	2	"	

As indicated in Fig. 3, the data by Forbes and associates are 16 per cent above the curves for our beef steers; the average of the metabolism data by Benedict and Ritzman is 16 per cent above our steer metabolism curve in the 600-700 kilogram region, and 13 per cent above in the 250 kilogram region.

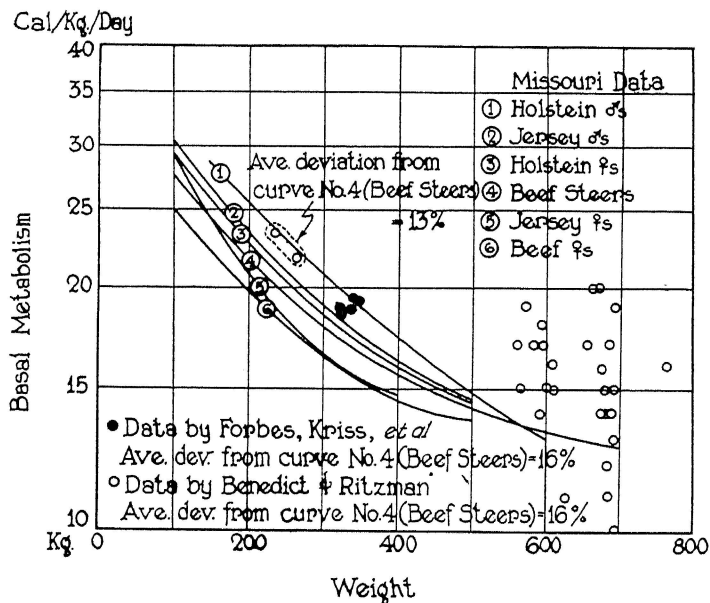


Fig. 3.—A comparison of the basal metabolism data of the several groups of our cattle (continuous curves), and of the data for beef steers by Benedict and Ritzman (light circles), and by Forbes, Braman, Kriss and associates (black circles). The data by the former are 13 and 16 per cent above our beef steer curve for the same weights; the data by the latter are 16 per cent above our beef steer curve.

Their higher values are easily explained by the fact that while our animals were lying, their animals were standing part of the time—and their values must, of course, include the work of standing up and lying down; also, our steers were fat, while theirs were thin.

The following statement appears in the publication referred to in the aforesaid table by Forbes and Kriss: "In consideration of the character of the component factors of the heat production of cattle, it is obvious that no short-time period of observation can be representative of a day's heat production". Since we use short-time periods of observations, we are under some obligation to defend our method. We may do this by saying that basal metabolism is not meant to represent a day's heat production, but the basal, or lowest metabolism; that is, the energy expense of maintenance when the animal is in its natural lying position, and absolutely quiet; and, of course, it is not possible to keep an animal in lying position and absolutely quiet during an entire day. A short-time period is therefore the *only possible* method for measuring *basal* metabolism.

BASAL METABOLISM AND HEAT INCREMENT OF FEEDING IN SHEEP

The sheep data, in Fig. 4a, have been treated in the same manner as the cattle data. The heavy broken curves represent resting metabolism. The data points below the resting curves represent observed basal metabolism data (fasted 48-72 hours). Each circle represents an individual measurement of an individual animal. The heavy continuous curves represent averages of the basal metabolism data. The very light broken lines represent "standard metabolism" values as given by Benedict and Ritzman, as will be presently explained.

The distribution of the data for the wethers is fairly uniform and consistent, the general basal-metabolism level being about 27 per cent less than the resting-metabolism level—the same as for cattle. Two data points (black circles) represent the metabolism of wethers when the animals fasted about 4 days, and were under complete amytal narcosis.

The distribution of the data for non-pregnant females is about the same as for the wethers. The gestation and lactation data are usually much higher, and irregularly distributed. The smooth curve for the females does not include the lactation or gestation data.

In this connection, we have plotted in Fig. 4b the recently published data on "standard" metabolism of sheep by Benedict and Ritzman and by Lines and Pierce. The very light lines in Fig. 4a represent the data of Benedict and Ritzman, as copied from this chart.

The distribution of the data by Lines and Pierce in the lower quadrant of Fig. 4b is too erratic for fitting an equation. The continuous

line drawn through these data is the average of the Benedict-Ritzman group of sheep. The broken line, which is about 20 per cent below the Benedict-Ritzman curve, represents in our opinion more nearly the average of the Lines-Pierce group of sheep.

The distribution of the Benedict-Ritzman data is fairly satisfactory, and we have fitted our equation (1) to their data as indicated on the chart.

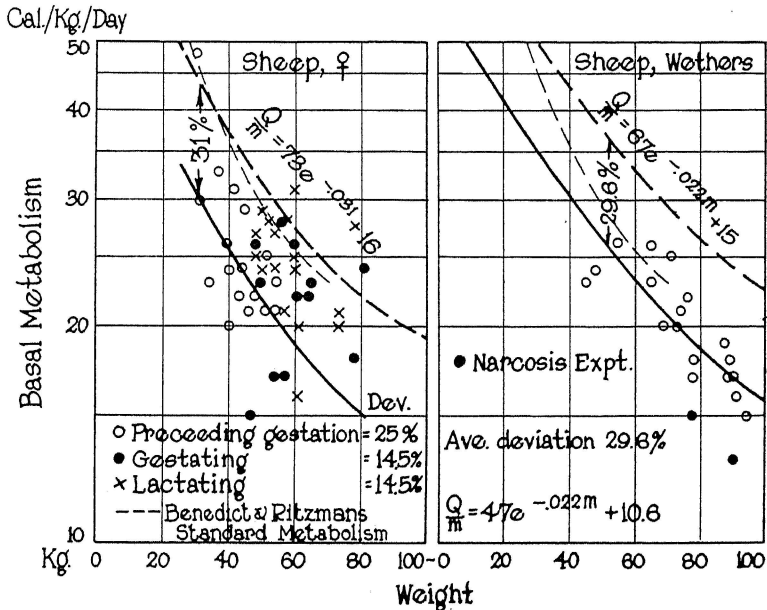


Fig. 4a.—The course of change of basal metabolism with increasing weight in sheep, females and castrated males. The circles and crosses represent individual observed values. The heavy broken curves represent *resting* metabolism. The smooth curves represent *basal* metabolism. The equations are given on the chart. Two wethers were fasted for about 100 hours and completely narcotized (the dosage was heavy enough to be fatal for one of these animals). The black circles on the wether chart show the results—the *basal* metabolism was lowered by about 20%. The very light broken lines represent the ‘standard metabolism’ values as given by Benedict and Ritzman and as explained in Fig. 4b. The smooth curve for the females represent the light circles only (preceding gestation). The gestation (black circles) and lactation (x’s) values are quite irregular and high.

Benedict and Ritzman’s “standard” metabolism is defined as the energy expended 24 hours after feeding in *standing* position. The measurements were made with the aid of a respiration chamber and gas analysis. Our data, on the other hand, represent metabolism in the lying (in the natural haunches position) position and 48 to 72 hours after feeding (*basal* metabolism), or about 12 hours after feeding (*resting* metabolism). Our measurements were made by the mask and oxygen spirometer method as previously described.

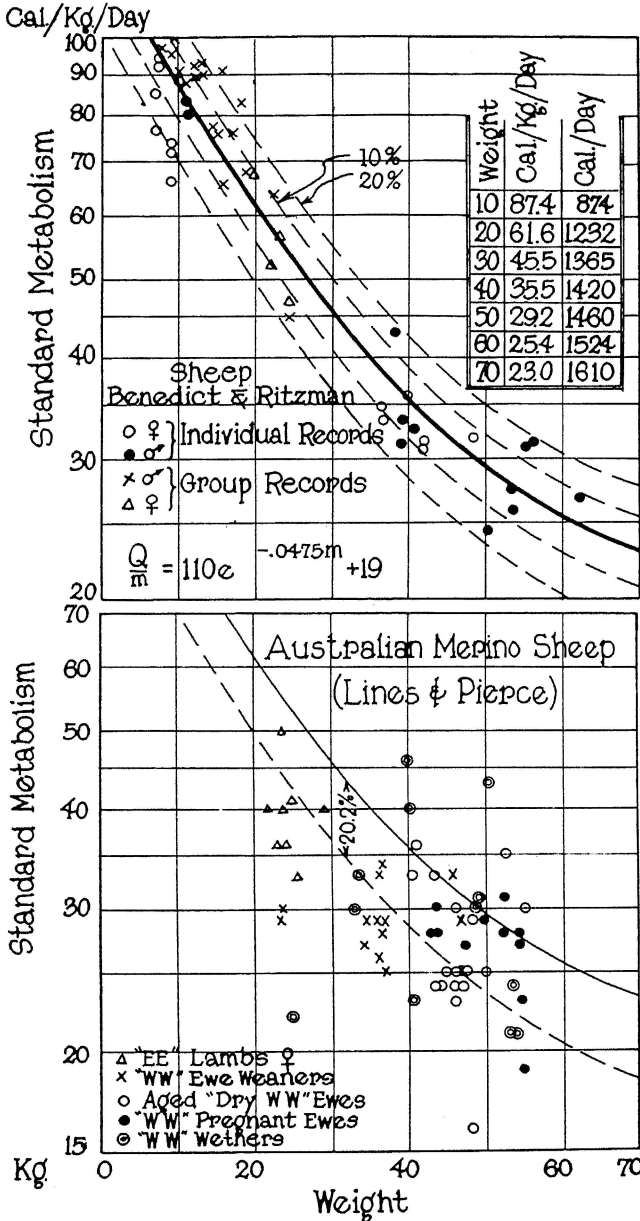


Fig. 4b.—The upper chart shows the course of *standard* metabolism with increasing weight in sheep, data by Benedict and Ritzman. The smooth curve represents the average; the broken curves represent 10 and 20% deviations from the average. The lower chart represents the data by Lines and Pierce. The smooth curve represents the average curve for the Benedict-Ritzman sheep; the broken curve (20% below the smooth curve) represents, in our judgment, the trend of the data by Lines and Pierce.

A numerical summary of resting and basal metabolism, and of the heat increments of feeding is given in Table 6.

TABLE 6.—RESTING METABOLISM, BASAL METABOLISM, AND HEAT INCREMENT OF FEEDING IN SHEEP

Weight Kgs.	Heat Production in Calories per Day					
	Resting Metabolism		Basal Metabolism		Heat Increment of Feeding	
	Females	Wethers	Females	Wethers	Females	Wethers
25	1240	1340	856	943	384	397
50	1575	1865	1087	1313	488	552
75	1740	2090	1201	1471	539	619
100	1930	2240	1332	1577	598	663

BASAL METABOLISM AND HEAT INCREMENTS OF FEEDING IN HORSES

We have plotted in Fig. 5 the curves of *resting* metabolism and data for *basal* metabolism of horses. The broken curves represent, as before, the resting metabolism, and the circles represent individual measurements of individual animals of *basal* metabolism.

The horse "basals" differ from the other species here discussed in the fact that the horses were measured while the animals were standing. Strange as it may seem, our horses made more fuss about lying down than any of the other farm animals, with the result that we decided to measure this species in the standing position, especially in view of the fact that horses, unlike other farm animals, rarely lie down. They apparently even sleep in the standing position, which suggests the thought that perhaps no greater amount of energy is required by horses for standing than for lying.

The distribution of the "basal" standing values is evidently not at all satisfactory. This may be attributed to a number of facts such as the "temperamental" nature of the horse as compared to other species, annoyance by horse flies in the warm weather (when most of the measurements were made), the habit of stamping the feet and switching the tail even in the absence of flies, then at other times going to sleep while the measurements were made. In other words, the irregularity of the distribution of the data is a reflection of the irregularity of the behaviour of the animals.

The geldings seem to have relatively lower "basal" metabolism values than the females. The average "basal" metabolism for females is 27 per cent less than the average of the resting values; those of the geldings is 35 per cent less than the resting. The fact that the percentage

difference between resting and basal metabolism is greater in the "half-fed" than in the "full-fed" group may probably be accounted for by the greater consumption of roughage by the half-fed group. The half-feeding refers to the grain only, both groups having free access to the roughage. The basal metabolism data on horses are admittedly unsatisfactory, and a great deal more work needs to be done on this species.

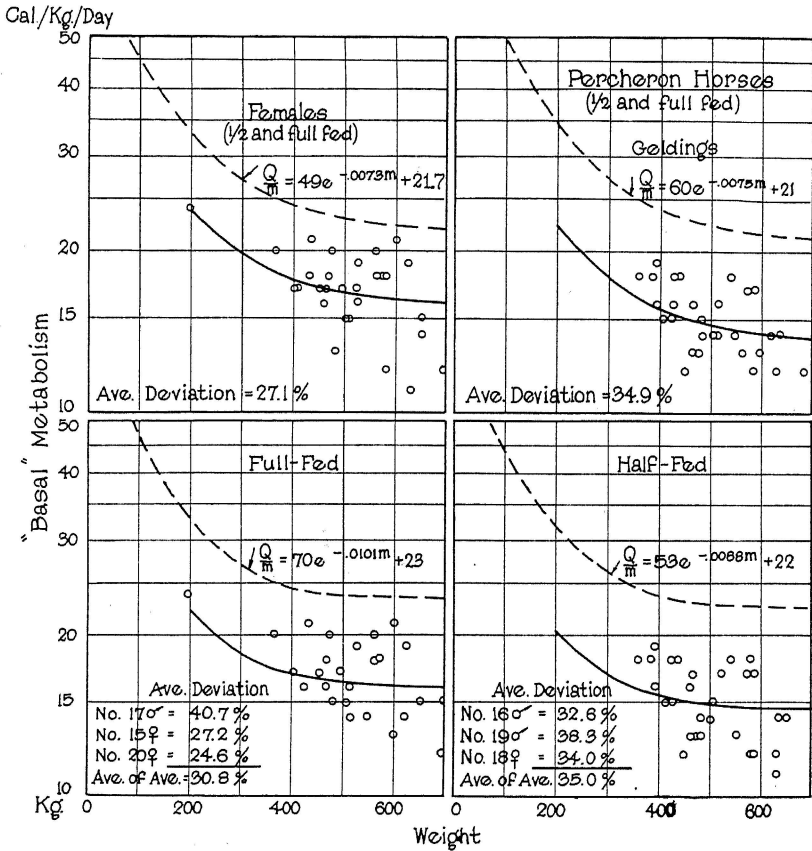


Fig. 5.—The metabolism of horses. The circles represent individual observed "basal" metabolism values. The broken curves represent the resting metabolism as determined in the preceding report.

Table 7 represents a numerical summary of the data charted in Fig. 5.

TABLE 7.—RESTING METABOLISM, BASAL METABOLISM, AND HEAT INCREMENT OF FEEDING IN HORSES

Weight Kgs.	Heat Production in Calories per Day											
	Resting Metabolism				Basal Metabolism				Heat Increment of Feeding			
	Full Fed	Half Fed	Fe- male	Geld- ings	Full Fed	Half Fed	Fe- male	Geld- ings	Full Fed	Half Fed	Fe- male	Geld- ings
300	7920	7740	8160	8190	5481	5031	5949	5332	2439	2709	2211	2858
325	8353	8125	8548	8515	5780	5281	6231	5543	2573	2844	2317	2972
350	8750	8540	8925	8855	6055	5551	6506	5765	2695	2989	2419	3090
375	9225	9000	9338	9225	6384	5850	6807	6005	2841	3150	2531	3220
400	9720	9440	9720	9600	6726	6136	7086	6250	2994	3304	2634	3350
425	10200	9903	10158	9988	7058	6437	7405	6502	3142	3466	2753	3486
450	10710	10350	10575	10350	7411	6727	7709	6738	3299	3623	2866	3612
475	11210	10830	11020	10783	7757	7039	8034	7020	3453	3791	2986	3763
500	11700	11300	11500	11206	8096	7345	8383	7291	3604	3955	3117	3909
525	12285	11813	11970	11603	8501	7678	8726	7554	3784	4135	3244	4049
550	12815	12320	12430	12100	8868	8008	9061	7877	3947	4312	3369	4223
575	13340	12823	12880	12535	9231	8335	9390	8160	4109	4488	3490	4375
600	13860	13380	13380	13020	9591	8697	9754	8476	4269	4683	3626	4544
625	14438	13875	13875	13438	9991	9019	10115	8748	4447	4856	3760	4690
650	15015	14430	14365	13975	10390	9379	10472	9098	4625	5051	3893	4877
675	15593	14985	14850	14445	10790	9740	10826	9404	4803	5245	4024	5041
700	16170	15470	15400	14910	11190	10055	11227	9706	4980	5415	4173	5204

BASAL METABOLISM, RESTING METABOLISM, AND HEAT INCREMENTS OF FEEDING IN SWINE

We have in Fig. 6a the curves of *resting* metabolism (heavy broken curves) and the observed data (circles) for *basal* metabolism of swine. The continuous heavy curves represent equation (2) fitted to the basal metabolism data. The very light broken and continuous lines represent respectively the "resting" and "basal" metabolism data of Deighton's castrated pigs as will be presently explained.

The distribution of the data is very regular, and the fit of equation (2) to the data is quite satisfactory.

A striking peculiarity of Fig. 6a is that the *percentage* difference between basal and resting metabolism decreases with increasing weight of the animal. The *absolute* difference between basal and resting metabolism tends to remain more constant.

Deighton has measured the metabolism of two pigs (castrated males) by a direct calorimetric (chamber) method at various times after feeding while the animals were asleep.

We plotted in Fig. 6b his data obtained within about 12 hours after feeding (light circles and light triangles) and also those obtained about 70 hours after feeding (black circles, and black triangles). We then fitted equation (2) to these data.

The average percentage difference between the resting and basal metabolism for Deighton's data is 31 per cent, which is of the same order

as the difference shown for our animals in Fig. 6a, that is 28 per cent for the males and 32 per cent for the female data. The resting and basal metabolism curves for Deighton's data (castrated males) are practically the same as of our resting female data. As shown in Fig. 6a,

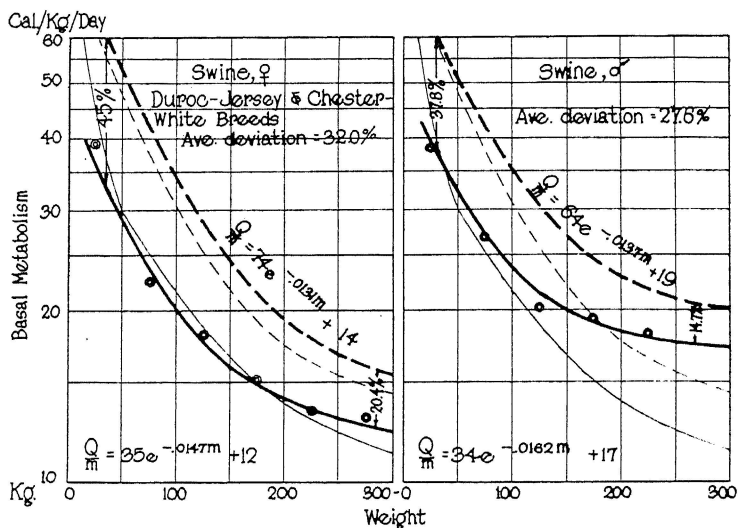


Fig. 6a.—The course of change of basal metabolism (circles and smooth curves) with increasing weight of swine. The heavy broken curve represents the *resting* metabolism data presented in the last bulletin, while the heavy smooth curve represents the *basal* metabolism data (circles). The very light broken and smooth curves represent respectively the resting and basal metabolism data by Deighton on castrated males, as given in detail in Fig. 6b.

the metabolism of our normal males, becomes increasingly higher with advancing weight than of Deighton's castrated males.

According to Deighton's values, shown in Fig. 6b, the resting and basal values are the same for the very early ages. This is a very significant fact. But with increasing age, the differences between basal and resting metabolism become more and more pronounced until body weight of about 50 kilograms is reached. After that, the slopes of the two curves are practically parallel on this arithlog grid, which means that the percentage difference between resting and basal metabolism is practically constant.

Unfortunately, our own data preceding 50 kilograms are too scanty for checking Deighton's findings in this respect.

In Table 8 we have tabulated the numerical values for all the swine data. The table in Fig. 6b is based on the given equations in this chart, fitted and computed by us. For purpose of easy comparison they are repeated in Table 8.

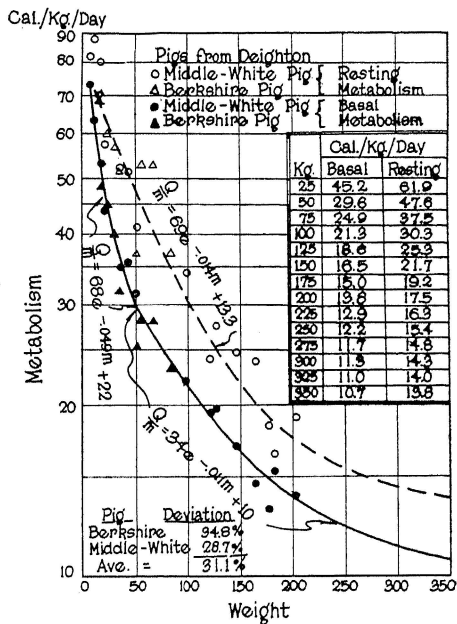


Fig. 6b.—“Resting” and “basal” metabolism data by Deighton on castrated pigs. The broken curve represents “resting” metabolism (measured about 12 hours after feeding). The smooth curve represents “basal” metabolism (measured about 70 hours after feeding).

TABLE 8.—RESTING METABOLISM, BASAL METABOLISM, AND HEAT INCREMENT OF FEEDING IN SWINE
(Heat Production in Calories per Day)

Wt. Kgs.	Resting Metabolism			Basal Metabolism			Heat Increment of Feeding		
	Fe-males	Males	Deigh-ton's	Fe-males	Males	Deigh-ton's	Fe-males	Males	Deigh-ton's
25	1680	1610	1548	905	993	1130	775	617	418
50	2620	2565	2380	1440	1605	1480	1180	960	900
75	3130	3140	2813	1770	2033	1868	1360	1107	945
100	3400	3530	3030	2010	2370	2130	1390	1160	900
125	3550	3810	3163	2200	2688	2325	1350	1122	834
150	3660	4080	3255	2385	3000	2475	1275	1080	780
175	3760	4340	3360	2573	3325	2625	1187	1015	735
200	3880	4640	3500	2780	3660	2760	1100	980	740
225	4005	4930	3668	2993	4028	2903	1012	902	765
250	4200	5250	3850	3225	4400	3050	975	850	800
275	4400	-----	4070	3465	-----	3218	935	-----	852
300	4650	-----	4290	3720	-----	3390	930	-----	900
325	-----	-----	4550	-----	-----	3575	-----	-----	975
350	-----	-----	4830	-----	-----	3745	-----	-----	1085

THE RELATION BETWEEN THE AVERAGE HEAT INCREMENTS OF FEEDING AND BODY WEIGHT

The heat increments of feeding (difference between resting and basal metabolism) of our various groups of animals are given in Table 9. In Fig. 7 the heat increments per unit of body weight have been plotted against body weight.

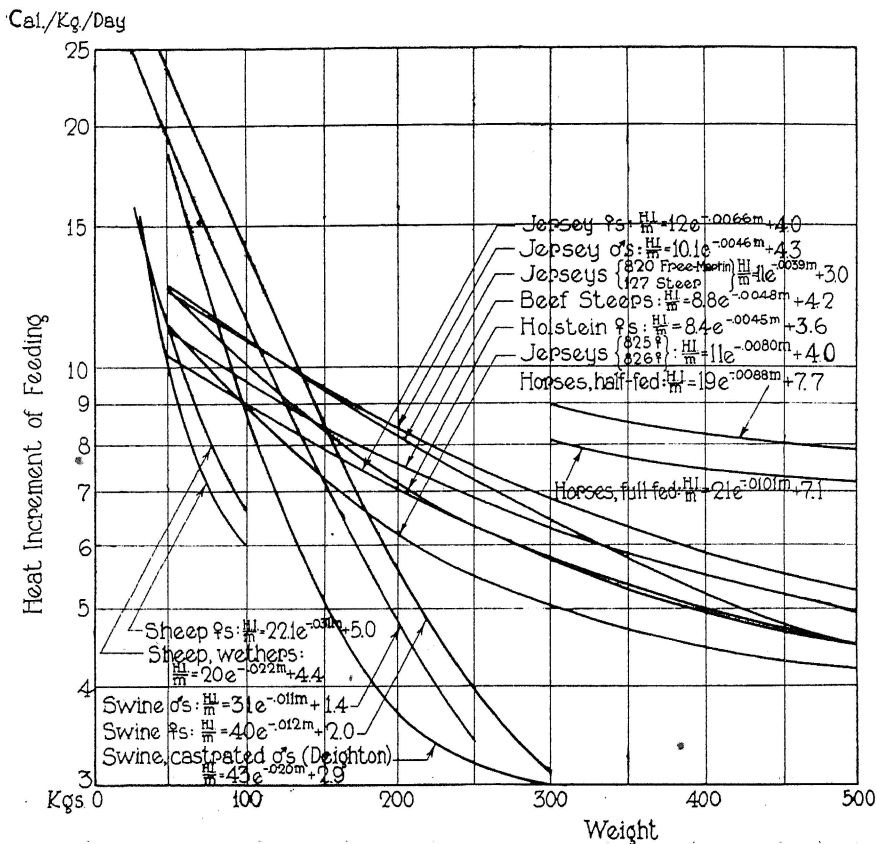


Fig. 7.—The heat increments of feeding in horses, cattle, sheep, and swine. The heat increments, $H. I.$, per unit weight, m , are plotted against the corresponding weights, m . The exponential equations (equation (2) in the text) are given for each curve. The slopes of these curves for heat increments of feeding are the same as the slopes for basal and resting metabolism.

Fig. 7 may be summarized as follows: (1) The heat increments of feeding *per unit of body weight* decrease exponentially with increasing weight; the increments decrease with increasing body weight at the same rate as do the resting and basal metabolism values per unit weight (the exponent, k , in the equation $Q/m = Ae^{-km} + C$ has the same

TABLE 9.—A SEX, GROUP, AND SPECIES COMPARISON OF THE HEAT INCREMENTS OF FEEDING

Heat Increment of Feeding, Calories per Kilogram per Day																
	Dairy Cattle					Beef Cattle		Sheep		Horses				Swine		
Wt. Kgs.	Hols. Fems.	Jersey Fems.	Jersey Males	Jersey Steer & Free-Martin	Under-fed Jersey Fems.	Here-ford Fems.	Here-ford Steers	Fems.	Weth-ers	Full Fed	Half Fed	Fe-male	Geld-ings	Fems.	Males	Deigh-ton's
25	11.1	13.9	13.5	13.5	12.9	29.6	12.0	15.4	15.9	---	---	---	---	---	---	16.7
50	10.4	12.4	12.5	12.5	11.3	25.1	11.1	9.76	11.0	---	---	---	---	---	---	18.0
75	9.64	11.2	11.6	11.6	10.0	21.2	10.3	7.19	8.25	---	---	---	---	18.1	14.8	12.6
100	9.01	10.0	10.8	10.8	8.9	18.1	9.62	5.98	6.63	---	---	---	---	13.9	11.6	9.00
125	8.41	9.17	10.1	10.0	8.0	15.3	9.03	---	---	---	---	---	---	10.8	8.98	6.67
150	7.89	8.41	9.47	9.36	7.3	13.1	8.47	---	---	---	---	---	---	8.50	7.20	5.20
175	7.44	7.76	8.89	8.74	6.7	11.1	7.98	---	---	---	---	---	---	6.78	5.80	4.20
200	7.04	7.20	8.40	8.20	6.2	9.50	7.54	---	---	---	---	---	---	5.50	4.90	3.70
225	6.66	6.73	7.93	7.69	5.8	8.09	7.18	---	---	---	---	---	---	4.50	4.01	3.40
250	6.33	6.32	7.56	7.24	5.5	7.10	6.81	---	---	---	---	---	---	3.90	3.40	3.20
275	6.02	5.99	7.18	6.81	5.2	6.11	6.52	---	---	---	---	---	---	3.40	---	3.10
300	5.76	5.71	6.86	6.43	5.0	5.30	6.27	---	---	8.13	9.03	7.37	9.53	3.10	---	3.00
325	5.55	5.47	6.57	6.11	4.8	4.70	6.01	---	---	7.93	8.75	7.13	9.14	---	---	3.00
350	5.32	5.27	6.33	5.78	4.7	4.10	5.80	---	---	7.70	8.54	6.91	8.83	---	---	3.10
375	5.15	5.09	6.09	5.51	4.6	3.70	5.62	---	---	7.58	8.40	6.75	8.59	---	---	---
400	4.95	4.94	5.91	5.25	4.5	3.30	5.47	---	---	7.49	8.26	6.59	8.38	---	---	---
425	4.81	4.81	5.72	5.03	4.4	3.00	5.30	---	---	7.39	8.16	6.48	8.20	---	---	---
450	4.69	4.70	5.56	4.82	4.3	2.80	5.17	---	---	7.33	8.05	6.37	8.03	---	---	---
475	4.55	4.63	5.43	4.63	4.2	2.60	5.07	---	---	7.27	7.98	6.29	7.92	---	---	---
500	4.48	4.55	5.29	4.44	4.2	2.40	4.97	---	---	7.21	7.91	6.24	7.82	---	---	---
525	---	---	---	---	---	---	4.86	---	---	7.20	7.88	6.18	7.71	---	---	---
550	---	---	---	---	---	---	4.78	---	---	7.18	7.84	6.13	7.68	---	---	---
575	---	---	---	---	---	---	4.71	---	---	7.15	7.81	6.07	7.61	---	---	---
600	---	---	---	---	---	---	4.65	---	---	7.12	7.81	6.04	7.57	---	---	---
625	---	---	---	---	---	---	4.60	---	---	7.12	7.77	6.02	7.51	---	---	---
650	---	---	---	---	---	---	4.55	---	---	7.12	7.77	5.99	7.50	---	---	---
675	---	---	---	---	---	---	4.50	---	---	7.12	7.77	5.97	7.47	---	---	---
700	---	---	---	---	---	---	4.47	---	---	7.11	7.74	5.96	7.44	---	---	---

value in the increment equation as in the basal and resting metabolism equations of the given animals). (2) For a given body weight and under the given conditions of feeding, horses seem to have the highest heat increments of feeding. However, this may be apparent rather than real because the relative degrees of rest or relaxation of the animal when measured for resting and basal metabolism inevitably influence the magnitude of the *apparent* heat increment. If the animals are more relaxed after a 48-hour fast than after a 10-hour fast (as they certainly are), then the apparent measured heat increment as given in Fig. 7 is higher than the real heat increment. The influence of fasting on the degree of relaxation seems to be greater for horses than for cattle. (3) The "half-fed" horses seem to have a higher heat increment of feeding than the full-fed horses, possibly because the half-feeding refers to grain only, and those half-fed with regards to grain consume more hay with a correspondingly higher heat increment of feeding. (4) The underfed dairy cattle (heifers 825 and 826) have a considerably lower heat increment of feeding than the normally-fed dairy cows because in the case of dairy cattle underfeeding, the underfeeding included hay as well as grain. (5) The Jersey male cattle appear to have a higher heat increment than the Jersey females probably because fasting quiets down the males to a relatively greater extent than it does the females, for the reason similar to that given for horses. (6) The sheep and swine can not be directly compared with cattle and horses because of differences in developmental age for given body weights. It is evident, however, that the larger and the older the animal, the less in proportion is its heat increment per unit weight; and that the rate of decline in the heat increment per unit of body weight is the same as the decline in basal metabolism. In other words there seems to be (as one might expect) a perfect adjustment between the food intake (with a proportionate heat increment) and the energy metabolism of the animal.

SUMMARY AND CONCLUSIONS

The essential and original contributions in this report are: (1) "Basal" metabolism data of large farm animals preceding age 3 years; (2) an equation relating resting and basal metabolism; (3) method of computing the average heat increment of feeding by difference between the resting, or the fairly constant general metabolic level, and the corresponding basal data; (4) indication that (following weaning) the heat increment of feeding tends to remain at a practically constant percentage level of the resting metabolism during the whole period of growth in ruminants and in horses, and that basal metabolism follows the same exponential course with increasing weight as does resting metabolism; (5) the value of the fairly constant heat increment of feeding in ruminants is of the order of 25 per cent of the resting metabolism; (6) the heat increment of feeding follows an exponential course with increasing weight of the animal in the same manner as does the basal, and also resting metabolism; that is, there is a direct proportionality between basal metabolism, resting metabolism, heat increment of feeding, and apparently food intake.

While it may be that the "basal" metabolism in ruminants is not strictly comparable to basal metabolism in man, we feel that the cause of this difficulty is inherent in the nature of the biological material rather than in the technique employed for measuring basal metabolism.

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XIX. Relation Between Basal Metabolism and Body Weight in the Growing Domestic Fowl.*

ABSTRACT

An analysis is presented for the energy metabolism of the domestic fowl covering the period from hatching until practical maturity. The metabolism per unit weight declines exponentially with increasing weight during growth. The metabolism of mature males is 8 to 10 per cent higher than of females. The metabolism of the heavy capons is somewhat below that of the females.

We have measured the energy metabolism of the domestic fowl with the apparatus shown in the following diagram (Fig. 1a). It is in principle, we presume, merely a large model of the modified Benedict-MacLeod apparatus, which is discussed in the following report on the metabolism of the white rat.

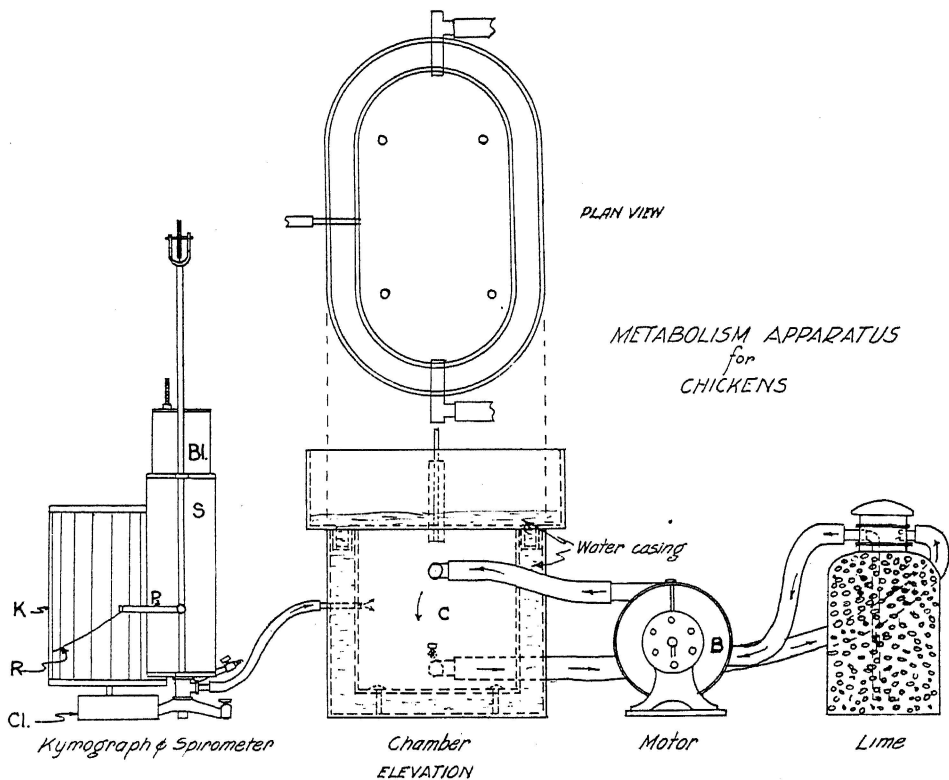


Fig. 1a.—Diagram of apparatus used for measuring heat production in the domestic fowl. The bird is placed in the water-jacketed chamber, C. The air is circulated by blower, B, through the soda lime where the CO_2 is absorbed. The rate of oxygen consumption is recorded graphically by the pen, P, on kymograph, K, actuated by clock, Cl.

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The bird is placed in the water-jacketed chamber *c*. The bell, *B*, floating in a water seal, *S*, is filled with oxygen, and as the oxygen is used up by the bird the bell sinks in its seal. A pen, *P*, is attached to the counterpoise weight, and as the bell sinks, the counterpoise weight rises, and the pen makes a graphic record, *R*, on the kymograph, *K*, actuated by a clock, *CL*. The rate of oxygen consumption, and therefrom the rate of metabolism is easily computed from the kymograph record.

The carbon dioxide is removed from the chamber air by circulating it by blower, *B*, through soda lime.

The metabolism values obtained by this method are too low, either because the CO_2 is not satisfactorily removed from the system, or because there is a tendency for an increase in the temperature of the system during the course of the run especially if the room temperature is relatively low; for these reasons, and because it is not possible to arrive at temperature corrections for this relatively complicated system, we have temporarily discarded this volumetric method in favor of the Haldane gravimetric method. Our metabolism values for chickens on pp. 178-179 Missouri Research Bulletin 143 and in this section are presented merely as a record of our work. We are frankly uncertain of their authenticity.

The data are presented in Fig. 1b. We have plotted in Fig. 1c, data by Mitchell, Card, and Haines.

The charts are self-explanatory. Our values are below those given by Mitchell and associates. The metabolism of the mature females is less than of males (about 8 per cent less) and the metabolism of the heavier capons is below that of the females.

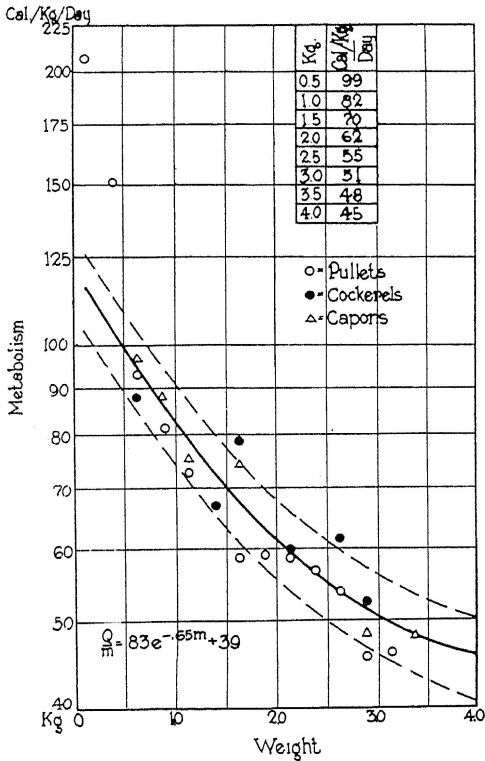


Fig. 1b.—The heat production in White Rock chickens, males, females, and capons. The broken curves represent $\pm 10\%$ deviations.

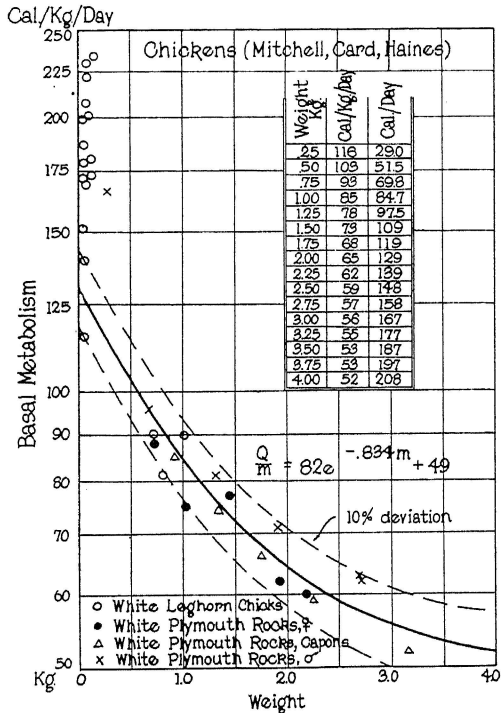


Fig. 1c.—The heat production in the domestic fowl as found by Mitchell and associates by the use of the Haldane gravimetric apparatus. Two breeds, both sexes and also capons, are included. Following 0.5 kg., all these data are within $\pm 10\%$ of the average curve. With increasing weight, the metabolism of the males steadily increases above the females or capons.

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XX. Relation Between Basal Metabolism and Body Weight in the Growing Rat.*

ABSTRACT

Data are presented on the basal metabolism in the normally-fed rat from birth to over one year of age. The metabolism per unit weight declines exponentially with increasing weight, the decline being of the order of 0.3 per cent for an increase in body weight of 1 gram. Data are also presented for a group of stunted rats (corn gluten constituting the only source of protein)—which gained only 60 grams from the time of weaning until one year of age.

DISCUSSION

The purpose of the investigation reported in this paper is to determine whether or not the energy metabolism in the white rat follows the same course with increasing weight as we have found to represent the metabolism in farm animals, and if so, to formulate equations representing the data.

Fig. 1a represents several groups of rats measured in this Station. Their metabolism was measured by the general method of Benedict and MacLeod, but with the following modifications in detail: (1) The oxygen consumption only was measured. (2) The decline in the oxygen spirometer was recorded graphically on a clock kymograph, the kind employed in connection with the Benedict-Roth-Collins clinical metabolism apparatus, and the rate of oxygen consumption was measured from the slope of the curve on the kymograph tracing. (3) The metabolism was computed on the assumption that the heat equivalent of oxygen is 4.825 Calories per liter (the animals were fasted 16 hours before measuring). (4) The oxygen consumption was measured for a period of 30 minutes, and the slope of the second 15-minute period was used for computing the metabolism. (5) The same animals were measured from birth until the present time (over a year). (6) The animals were measured in groups during their periods of nursing, and individually following this period.

In connection with another investigation, the 5 groups of rats shown in Fig. 1a were grown on different diets; and these diets were changed from time to time (as indicated on the chart) for the purpose of the other investigations.

The lower left quadrant (No. 1) represents the average of 5 rats grown on a "high protein" stock diet, with occasional periods on a

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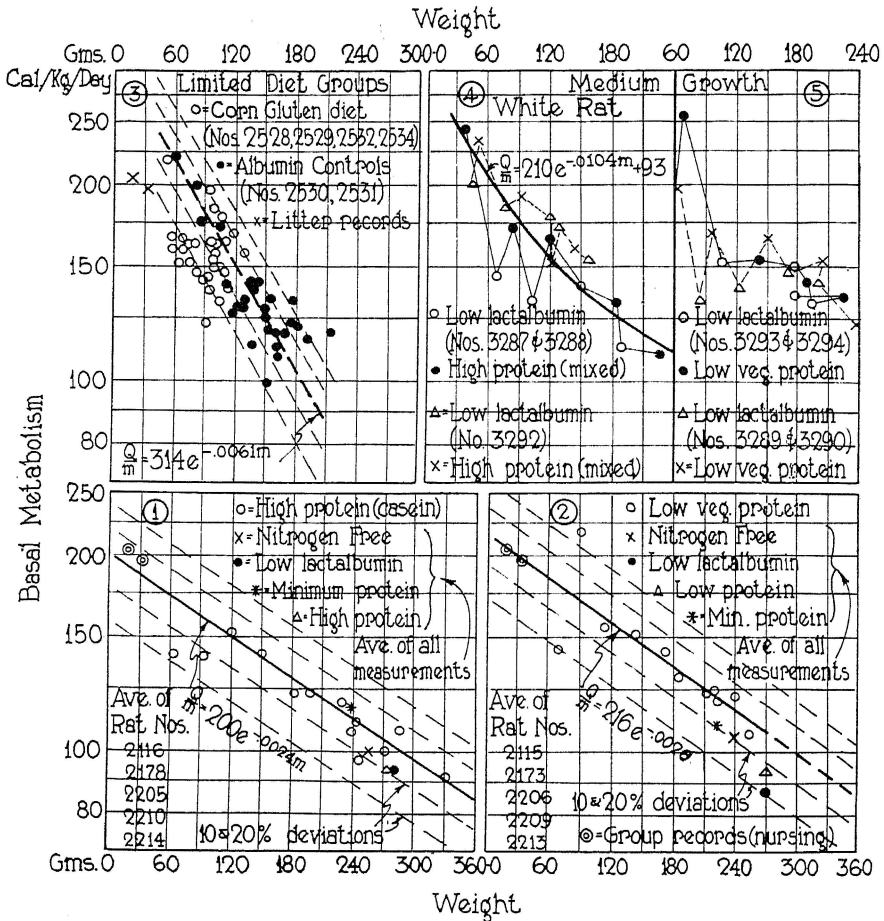


Fig. 1a.—The course of metabolism with increasing body weight of 5 groups of rats on different diets. From the present point of view, only the lower quadrants (1 and 2) are significant, indicating the course of change of energy metabolism with increasing weights in rats growing on a more or less complete diet. The complete diets are frequently interspersed with periods of feeding with incomplete diets. The animals in quadrant (3) are stunted, and are made up of two groups of rats on different qualitative diets. The equation of this group is therefore not typical. The same is true of the data in rectangles (4) and (5) which will be discussed elsewhere in greater detail.

nitrogen free diet and on a low-lactalbumin diet. The smooth curve represents the average of all the data; the broken curves represent 10 and 20 per cent deviations from the average. The average curve is represented by the equation

$$Q/m = 200e^{-0.0024m}$$

in which Q/m is the heat production per unit weight for weight m ;

e , is the base of natural logarithms; the value .0024 means that the metabolism per kilogram declines at 0.24 per cent per gram increase in body weight (or 240 per cent per kilogram increase in body weight). It is equation (1) in the text of the first paper in this bulletin.

The same interpretations hold true for the "low protein" group (the lower right quadrant, marked No. 2).

The upper left quadrant (No. 3) represents animals (light circles) kept on a diet in which corn gluten (an incomplete protein) is the sole source of nitrogen; and also control rats (dark circles) which had an equivalent amount of lactalbumin (a complete protein) as source of protein but the feed intake of which was quantitatively limited to the amount taken by the corn-gluten group.

The gluten-fed animals gained relatively very little (from 60 to 120 grams) from the age at weaning to one year. The purposes of keeping these animals at this nearly constant body weight, were (1) to determine whether the change of metabolism per unit weight with increasing weight is caused, functionally, by increase in body weight, or by the increase in age which accompanies increasing weight; and (2) to compute the energy cost of growth as distinguished from maintenance. These problems will be discussed in detail in a future report.

The curves on quadrants (4) and (5) in Fig. 1a represent animals kept on special diets. They do not call for discussion at the present time.

Fig. 1b represents published data on the basal metabolism of the white rat by Mitchell and Carman (left quadrant) and by Benedict and MacLeod (right quadrant).

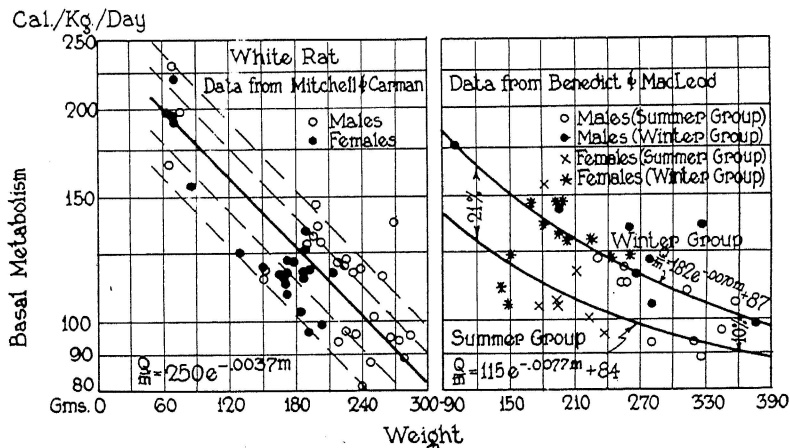


Fig. 1b.—Metabolism per unit weight with increasing weight of rats measured by Mitchell and Carman (left rectangle) and Benedict and MacLeod (right rectangle). As usual, males have a higher metabolism than females.

Fig. 1c represents graphic and numerical comparisons between the several groups of our animals, and those of Benedict and MacLeod, and of Mitchell and Carman. It is clear from this chart that the winter group of Benedict and MacLeod has the highest metabolic level, and their summer group has the lowest metabolic level. Our "normal" curves fall between the winter group of Benedict and MacLeod, and the average of Mitchell's and Carman's data. (We are excluding from discussion at this time our limited-diet group.) It is of some theoretical

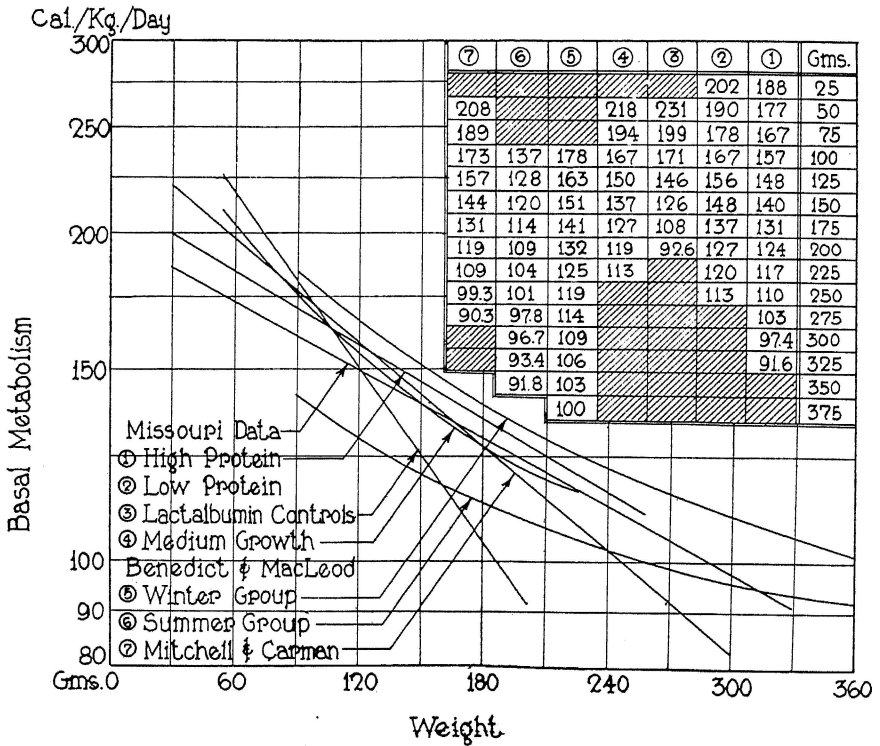


Fig. 1c.—A comparison of the metabolism curves of our rats on the several diets with those of Benedict and MacLeod, and of Mitchell and Carman. The table on the chart gives a numerical comparison. The weights are tabulated in the right column and the metabolism (Calories per kilo per day) in the other columns.

interest and practical importance to note that our rats on the "high protein" diet are heavier and appear to be fatter than those on the "low protein" diet, and that perhaps for this reason the basal metabolism of our rats on the high protein diet is lower than of the rats on the "low protein" diet. It is not clear why the "high-protein" rats should be fatter, or larger, than the "low-protein" rats in view of the fact that both

groups were paired to diets of the same energy content per day, and no extra allowance was made for the supposedly higher heat increment of feeding of the high protein diet.

Following is the composition of each of the rations fed to the several groups of rats:

TABLE 1.—RATIONS FED TO THE SEVERAL GROUPS OF RATS

	Min. Prot. Diet	Low Veget. Prot. Diet	High Prot. Veget. Diet	High Prot. Casein Diet
Whole Wheat.....	20.0	60.0	60.0	10.0
Alfalfa meal.....	2.5	2.5	2.5	---
Dried yeast.....	10.0	10.0	10.0	10.0
Salts (14A).....	2.5	2.5	2.5	4.0
Casein.....	---	---	20.0	70.0
Starch.....	60.0	20.0	---	---
Butter.....	4.0	4.0	4.0	2.0
Cod liver oil.....	1.0	1.0	1.0	2.0
Cellulose.....	---	---	---	2.0
	100.0	100.0	100.0	100.0
Nitrogen content (mg/gm).....	13.0	20.0	49.0	95.0

	Low Lact- albumin diet	N-free diet	Corn gluten diet	Albumin diet controls for the gluten group
Starch.....	71	74	59	65
Sucrose.....	10	10	--	--
Lactalbumin.....	2	--	--	14
Salts (14A).....	4	4	4	4
Cellulose.....	3	2	2	2
Butter fat.....	8	8	--	--
Cod liver oil.....	2	2	2	2
Corn gluten.....	--	--	20	--
Lard.....	--	--	13	13
	100	100	100	100
Nitrogen Content (mg/gm)---	2.5	0.5	17.0	17.0

SUMMARY AND CONCLUSIONS

The decline of basal metabolism with increasing weight in the white rat follows an exponential course, and is satisfactorily represented by equation (1) in the text, namely $Q/m = Ae^{-km}$. The value of k is of the order of 0.003 which means that the metabolism per unit weight declines at the rate of 0.3 per cent per increase in 1 gram in body weight.

The basal metabolism of fully grown rats is between 90 and 100 Calories per kilogram per day; while of nursing rats it is of the order of 200 Calories per kilogram of body weight.

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XXI. Relation Between Basal Metabolism and Body Weight in Man; Published Data.*

ABSTRACT

The basal metabolism of humans follows an exponential course with increasing weight during the weight interval 10 to 110 kilograms, according to the equations $Q/m = 49e^{-.035m} + 20$ for males, and $Q/m = 50e^{-.027m} + 13$ for females. Q is the heat production per day per kilogram m. About 78 per cent of the data are within ± 10 per cent of the computed average and 99 per cent within ± 20 per cent of this average. The apparently low efficiency of growth in humans (as pointed out by Rubner) is a consequence of the relatively low rate of growth of this species, and consequently of the greater energy expenditure for maintenance while making the relatively slow gains in body weight. Sex and race differences are discussed.

INTRODUCTION

The present communication is presented partly in order to substantiate the apparent fact (found while analyzing metabolism data of farm and laboratory animals) that energy metabolism follows an exponential course with increasing weight; and partly because of the inherent interest in human metabolism. We have shown in Missouri Research Bulletin 104, that the course of growth in weight of man is quite different from the course of growth in weight in all other species examined. One's curiosity is therefore naturally aroused as to what might be the relation between the metabolism of humans and other species examined. This interest is heightened by the fact, found by Rubner, that the human child occupies a unique position with regard to its efficiency of growth. While the human infant utilizes only 5 per cent of its food (milk) energy for growth, the young of other species utilize about 34 per cent of their food (milk) energy for growth. In other words, while the human infant requires about 29,000 Calories of food energy to double its birth weight, other species examined required only about 4000 Calories to double their birth weight.

DATA AND CHARTS

Following the infantile and early childhood periods, the human subject is of all species the most ideal subject for basal metabolism investigations, first, because the post-absorptive state in this species is a normal daily occurrence and it is easily attained; second, because of the relative ease with which the cooperation of the subject is secured. For these, and for medical reasons, there has been built up a great body of data on basal metabolism of humans.

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Of all the published data on basal metabolism of humans the most extensive and the best known series of measurements are due to Benedict and his associates. We have therefore examined these data and supplemented them, by way of check, with some data by Boothby and Sandiford. Benedict's data include the material published in Carnegie Institution Publications 279 (1919) and 302 (1921); and Series II, 1928, in which "individuals of unusual configuration have been included".

The data (individual measurements) are exhibited graphically in Figs. 1a (American white males); 1b (American females); and 1c (Australian aboriginals).

About 75 per cent of the data of the heterogeneous American population come within ± 10 per cent of the average curve and about 99 per cent within ± 20 per cent; but about 85 per cent of the data of the more homogeneous Australian population are within ± 10 per cent of the average curves. In other words, the agreement between observed and computed values is very good for a genetically homogeneous population, and satisfactory for a genetically heterogeneous population, such as one finds in the great American cities (Boston, Massachusetts, and Rochester, Minnesota). The agreement between observed and computed values might be still bettered by fitting the equation by least square methods (involving more time for computation than we can afford to give).

The equation for each curve is given on the charts, and it has been discussed in the text in the preceding communications of this series.

Fig. 1c also shows the average curves for men and women taken from Figs. 1a and 1b. They are shown by very light lines, and for the purpose of comparing the metabolism of American men, women, and the Australian aboriginals. The conclusions of the comparison are clear and need but few comments: The metabolism of American males is at all weights (and ages) higher than that of American females; and this difference steadily increases with increasing body weight. The metabolism of American males is somewhat less than the metabolism of Australian males in the earlier ages; but beginning with body weight of about 40 kilograms, the metabolism of American males grows continuously greater than the metabolism of Australian males. The curve of American females is below that of Australian males for all weights but the larger the weights the more closely do the two approach each other. While it is not the function of this communication to interpret these peculiarities, outside of demonstrating the fact that the course of basal metabolism with increasing weight in man follows an exponential course, it is somewhat difficult to resist the temptation of pointing out the relative influence of body weight (and of course age) on the relative metabolism

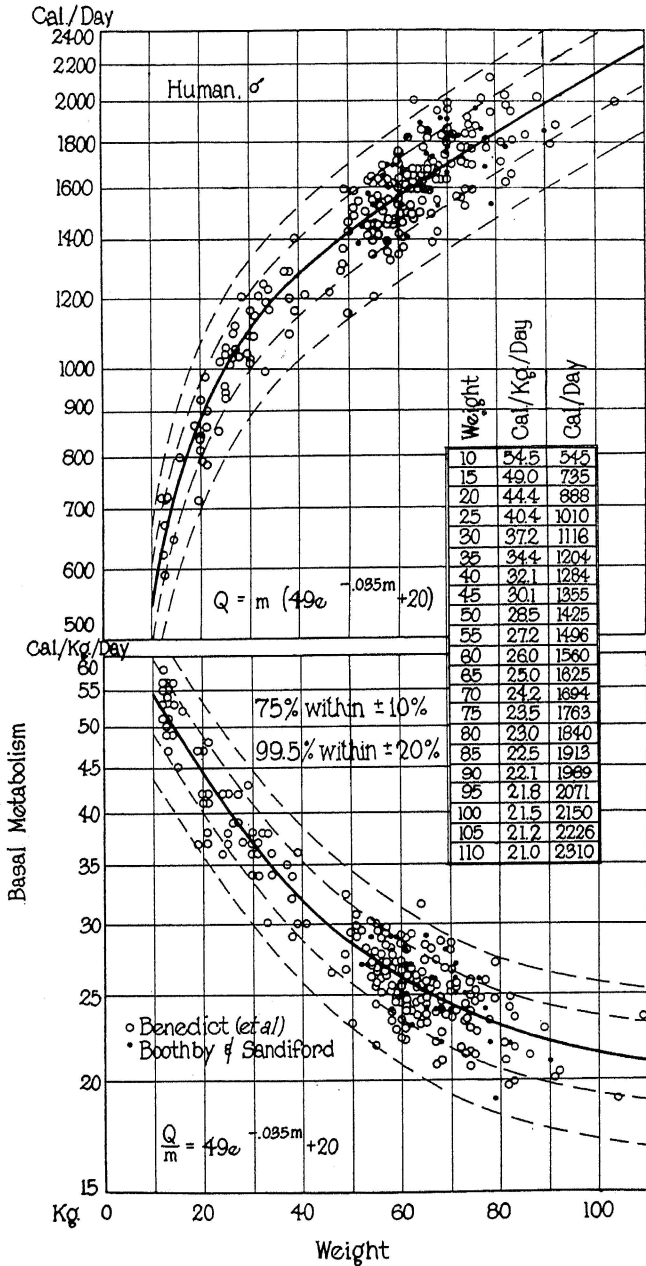


Fig. 1a.—The course of basal metabolism with increasing body weight in humans, American white males. Large light circles represent individual measurement by Benedict and associates; small black circles represent individual measurement by Boothby and Sandiford. The continuous curves represent the equations given on the chart. The broken curves represent 10 and 20% deviations from the average. The declining curve represents metabolism per kilogram per day; the rising curves represent metabolism per individual per day.

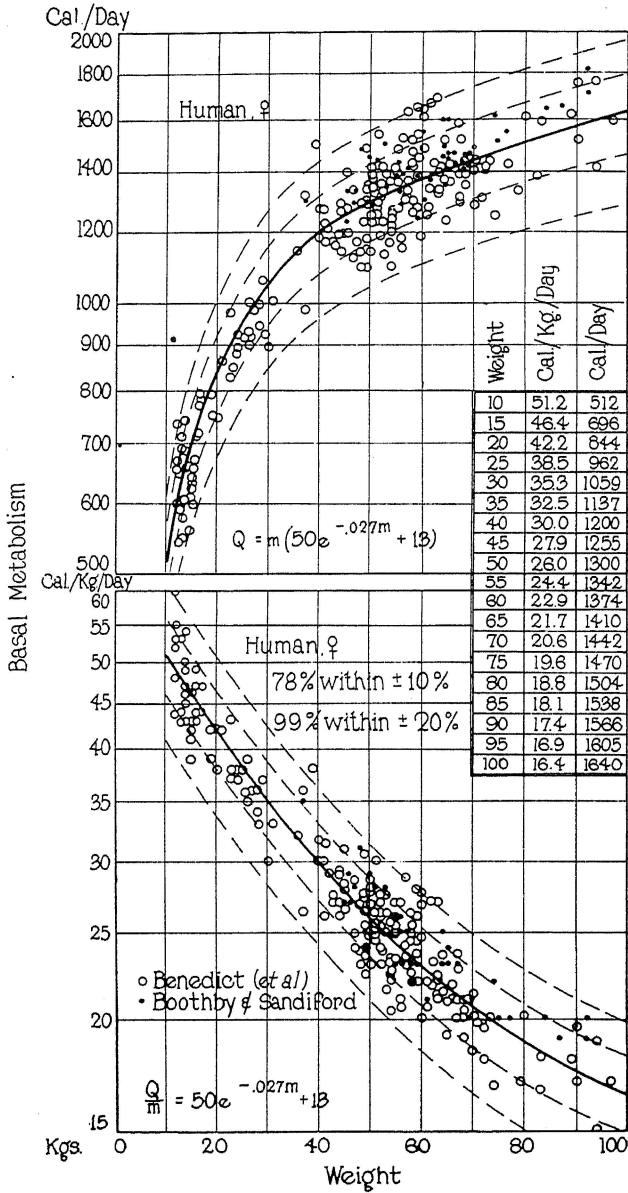


Fig. 1b.—The course of basal metabolism with increasing weight in humans, American white females.

of human males and females—and incidentally, on white and Australian males. This is accordingly shown in Fig. 1c and Table 1. It is there seen that the metabolism curves of American children are nearest together between 20 and 30 kilograms (7 to 13 years), after which the sexes diverge

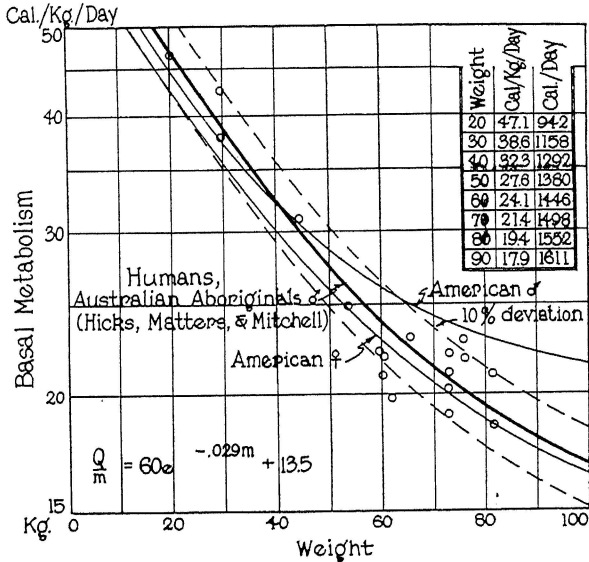


Fig. 1c.—The course of basal metabolism with increasing weight. Australian Aboriginal males. The circles represent observed values; the continuous curve represents the equation given on the chart; the broken curves represent 10% deviations from the average.

The light continuous curves are reproduced from Figs. 1a and 1b and represent respectively, for purposes of comparison, the basal metabolism of American males and females.

These Australian natives "are all pure-blooded aboriginals of the Kokkata tribe, collected at the Koonibba Mission of the Evangelisch Lutheranische Kirche of South Australia".

TABLE 1.—THE INFLUENCE OF SEX AND RACE ON THE RELATIVE BASAL METABOLISM OF AMERICAN (WHITE) MALES AND FEMALES, AND AUSTRALIAN ABORIGINAL MALES

Weight, Kilograms.....	10	15	20	30	40	50	60	70	80	90	100
Per cent Basal Metabolism of Females to Males (Am. White).....	93.9	94.7	95.0	95.0	93.5	91.2	88.1	85.1	81.7	78.8	76.3
Per cent Basal Metabolism of Australian Male to American Male.....	----	----	106	104	101	96.8	92.7	88.4	84.3	81.0	----
Per cent Basal Metabolism of American Female to Australian Male.....	----	----	89.5	91.5	92.9	94.2	95.0	96.6	96.9	97.2	----

more and more with increasing weight. The metabolism curves of Australian and American men are nearest together in the region of 40 kilos (14-15 years), after which there is a steady divergence. The divergence in both cases (male-female comparison and American-Australian males comparison) begins at puberty. The larger the body weight, the greater the difference in metabolism between American males and American females; but, also, the larger the body weight the less the difference in metabolism between American females and Australian Aboriginal males. The significance of these differences is perhaps this: The female reaches maturity and her mature weight earlier than the male; so that for a given weight the American white female is in a more advanced physiological age than the American white male; and the Australian male is probably also, for a given weight (following puberty), in a more advanced physiological age. Hence the lower metabolism of American females, and Australian males than of American males. Of course, the problem of adiposity might also enter as a factor.

SUMMARY AND CONCLUSIONS

The basal metabolism of humans follows an exponential course with increasing weight (from 10 to 110 kilograms) in the same manner as does the basal metabolism of other species, and particularly of sheep which have the same weight range during postnatal life as men. The differences in efficiency of growth between humans and other species as pointed out by Rubner, is due not to differences in the intensity of basal metabolism nor to differences in the efficiency of food utilization, but to differences in the rate of growth with the accompanying *differences in energy cost of maintenance* during a given increase in body weight (depending on whether the gain in body weight is made in a short or long time interval). An incidental but very suggestive fact relating to sex and race difference is discussed.

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XXII. Relation Between Basal Metabolism and Body Weight in Laboratory Animals; Published Data.*

ABSTRACT

The exponential equation which was found to represent the metabolism with increasing weight of growing animals also appears to represent satisfactorily the relation between metabolism and weight in relatively mature dogs. Of all animals examined the dove appears to suffer the greatest decline in metabolism with increasing weight during growth—the same species which was previously shown to approach maturity with the greatest speed. This suggests that the percentage decline in metabolism with increasing weight tends to be proportional with the percentage decline in the rate of growth with increasing age.

THE DOG

For this purpose we examined the classic data of Rubner, used by him as a basis for the formulation of the surface law, and the more recent American data. The data here presented are taken from the compilations by Kunde and Steinhaus and by Kraus.

The older values for metabolism are naturally higher than the recent American figures, for the reason that the condition of complete rest was not then adhered to. We have therefore drawn in Fig. 1a, two separate curves, the upper one representing the older data and the lower curve representing the newer data. The broken curves represent 10 per cent deviations from the average. It appears that considering the variety of sources of the data, and the heterogeneous nature of the populations, represented, the agreement between observed and computed values is satisfactory.

THE GUINEA PIG

The data are plotted in Fig. 1b. The data by Ginglinger and Kayser represent young animals. The other animals represented in the chart are presumably mature. Most of the data points are seen to be within ± 10 per cent of the average. We think that the agreement between observed and computed values is satisfactory. With the exception of the data by Ginglinger and Kayser, the values were taken from Kraus' compilation.

THE RABBIT

The data are plotted in Fig. 1c. We did not find it possible to represent all the groups of data by one equation. Most of the data by Ginglinger and Kayser are for very young animals, and they had to be represented by a curve all by themselves. The other data are represented

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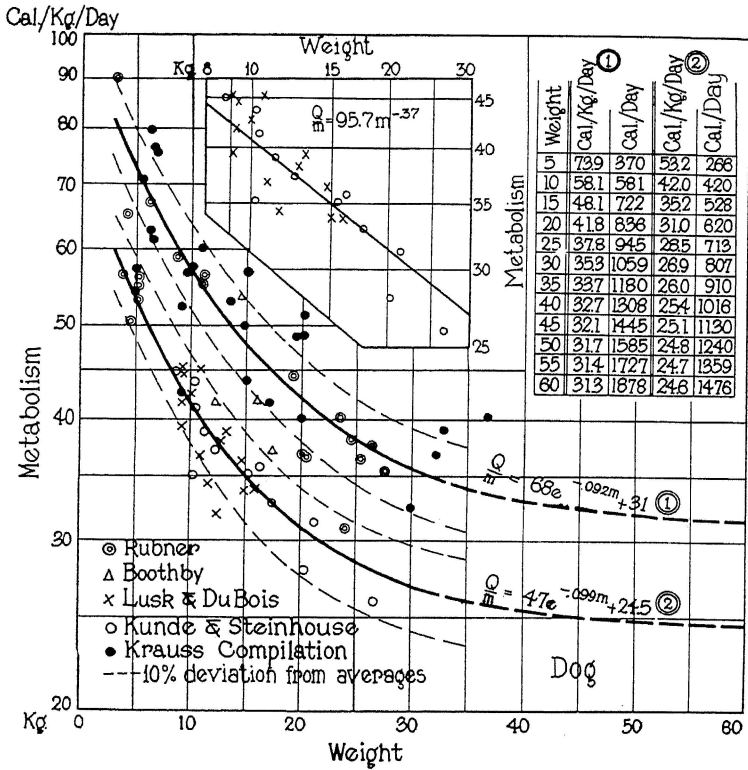


Fig. 1a.—The metabolism of mature dogs of different body weights. The lower curve represents basal metabolism data. Rubner's data and the Kraus' compilation data were obtained mainly at the time when the condition of absolute rest was not yet strictly adhered to. The lower group of data fall within $\pm 10\%$ of the average exponential curve. The inset shows the American data (Calories per kilogram per day against weight) plotted on log-log paper. The equation for Calories per kilogram per day plotted against weight is $Q/m = 95.7m^{-.37}$, in which Q is the heat production for body weight m . If the total metabolism were plotted against weight, the equation would be, of course, $Q = 95.7m^{.63}$.

by another equation, and the data are within ± 20 per cent of the average. The agreement between observed and computed values is perhaps not bad considering the variety of sources, and variety of methods by which the measurements were carried out. With the exception of the data by Ginglinger and Kayser, the values were taken from the compilation by Kraus.

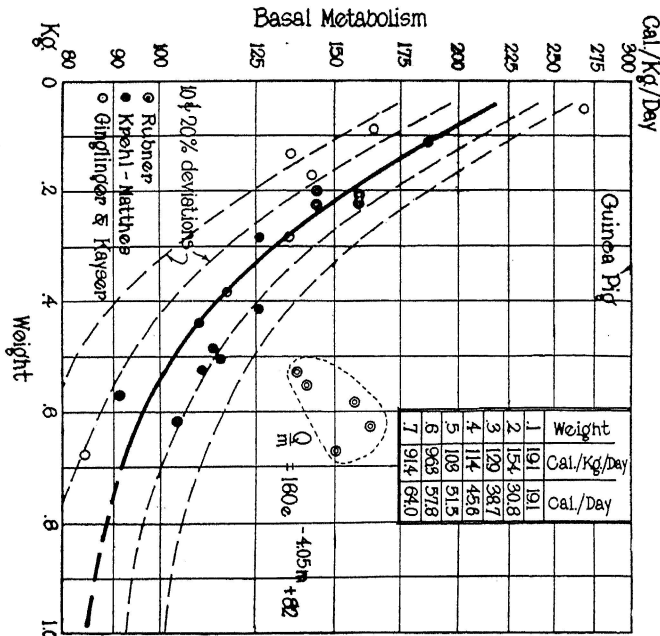


Fig. 1b.—The metabolism of the guinea pig. The enclosed group of points in the .5-7 kilogram region represent measurements on the same animal.

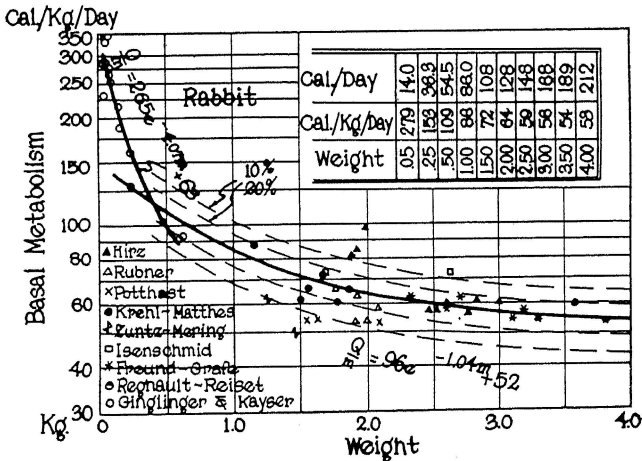


Fig. 1c.—The metabolism of the rabbit. Note that the young animals measured by Ginglinger and Kayser had to be represented by a different curve.

PIGEON AND DOVE

These data are by Riddle, Smith, and Benedict, and they were kindly sent to us by Dr. Oscar Riddle at Professor Benedict's request. The birds were measured at night at a temperature of 30° C., and "these are really basal data" (quoted from a letter by Dr. Riddle).

The data are plotted in Fig. 1d. Since the range in weight is relatively narrow, therefore their distribution on coordinate arithmetical paper would probably be as good as on semilog paper; so this chart can not be said to substantiate the validity of the proposed exponential equation. However, the chart is here presented, because the numerical values of the exponent (k in the equation in the text) might be of interest.

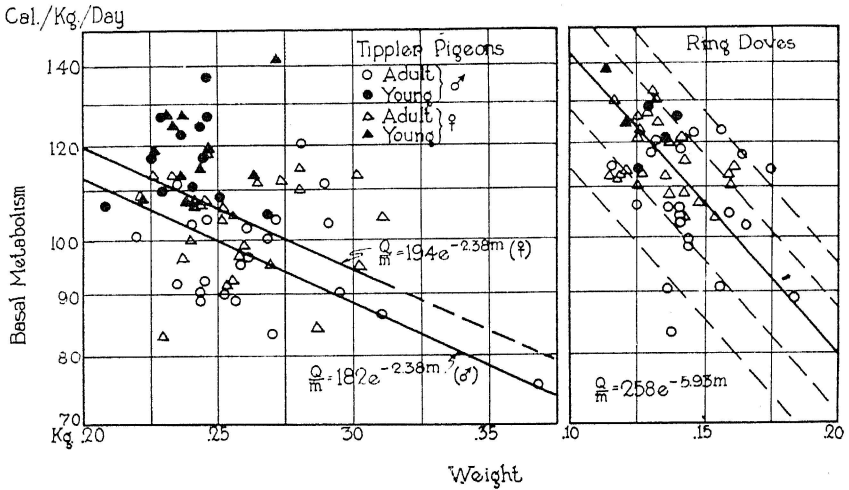


Fig. 1d.—The metabolism of the pigeon and dove (data by Riddle, Smith and Benedict). The broken lines on the right represent 10 and 20% deviations from the average.

We have shown in Missouri Research Bulletin 101 (Page 14) that of all species examined the dove approaches maturity with the greatest speed. It is therefore of great interest to know that the exponent in our exponential equation (1) for decline of basal metabolism with increasing weight in the dove is likewise the highest we came across. The metabolism in the dove declines with increasing weight at the rate of 593 per cent for an increase (theoretical) in body weight of one kilogram.

As pointed out to us by Dr. Riddle, the young birds are seen to have a higher metabolism than mature birds. The numerical values of the constants of the equation (fitted by inspection) are the same for the male and female dove; but in the case of the pigeon, the female appears

to have a higher metabolism than the male. In the case of the other species examined, the males were found to have a higher metabolism.

SUMMARY AND CONCLUSIONS

It appears that the exponential relation between basal metabolism and body weight represents not only the metabolism of young animals, but it also represents the metabolism of approximately mature animals of the same species, as in the dog. The decline of metabolism with increasing weight is characteristic of each species depending on the rate with which maturity is approached. The more rapidly an animal matures, the more rapidly does its metabolism per unit weight decrease with increasing weight. Thus, the dove approaches maturity at the most rapid rate, and its decline of metabolism with increasing weight is also most rapid.

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XXIII. Relation Between Basal Metabolism and Mature Body Weight in Different Species of Mammals and Birds.*

ABSTRACT

The basal metabolism of mature domesticated animals increases with the 0.734 power of body weight; of "Wild" birds it increases with the 0.64 power of body weight; of mammals and birds combined, it increases with the 0.685 power of the body weight. The metabolism per unit weight raised to the above powers is respectively 70.4; 89, and 86.5. Practically all the observed values are within ± 20 per cent of the above equation values. The average percentage deviations of the observed from the equation values are respectively 10.3, 17.9, and 18.6. Over 50 different species of mammals and birds are included in the above equations, ranging in body weight from 10 to 1,000,000 grams, and ranging in metabolism from 4 to 10,000 Calories per day. The metabolism-weight curves of *growing* animals do not coincide with and do not have the same slope as the metabolism-weight curves of mature animals of different species. It is suggested that metabolism during *growth* is an exponential function of body weight, and metabolism of different *mature* species is a power function of body weight. The greater the rapidity with which a species reaches its maturity, also the greater the rapidity with which its metabolism declines with increasing weight. The metabolism per unit weight is a function of the size of the species and also of its state of maturity. Among domestic animals swine and sheep appear to have the relatively lowest metabolism; cattle and horses the highest metabolism.

INTRODUCTION

Having determined the law relating metabolism to body weight during *growth* in members of the *same* species, we next proceed to relate metabolism to body weight of *mature*, or practically mature, animals of *different* species.

It is made clear that the exponential equation used in the preceding papers of this volume was proposed to relate metabolism to weight during active *growth*. The exponential equation was chosen for this purpose partly in order to bring out the similarity between the decline in the rate of metabolism per unit weight with increasing size of the animal to the decline in the rate of growth with increasing size; but mainly, of course, because this form of equation best represents the data.

Experience has shown that as regards relating metabolism to body weight in *mature* animals, especially if they are of different species, success is more likely to be attained by the use not of an exponential equation of the form

$$Q/m = Ae^{-km} \quad (1)$$

*Paper No. 43 in the Herman Frasch Foundation Series.

which is equation (1) in the text, but rather by a power function of the form

$$Q/m = Am^{-k} \quad (3a)$$

or, what is the same,

$$Q = Am^k \quad (3b)$$

As before, Q is the heat production, m is the mass, or body weight, A and k are constants not at all related to the A and k of equation (1). The k of equation (3a) equals $1-k$ of equation (3b).

The historical reasons for choosing equation (3) for relating metabolism to weight in mature animals may be found in the very admirable recent paper by Kleiber.

Kleiber has indeed attempted to determine the best values of the constants k and A in the above equation (3b) by using a method of trial and error and then testing the goodness of the results of the various trials statistically. Several years ago, Brody, Comfort, and Matthews have attempted to do the same thing, in a more elementary fashion by a graphic method.

In this paper, we shall attempt to extend this work and again partly by a graphic method, but also partly by a statistical method.

Our method of evaluating k and A hinges on the fact that equation (3b) if written in the form

$$\log Q = \log A + k \log m \quad (3c)$$

shows that $\log Q$ when plotted against $\log m$, gives a straight line. The same results may, of course, be attained by plotting Q (metabolism) against m (weight) on logarithmic coordinate (or log-log) paper. In the past work we had fitted equation 3b by thus plotting the data on log-log paper then fitting the equation by the method of selected points. The linear form of the formula, (3c), may likewise be used conveniently for fitting the power equation to the data by the method of least squares as applied to linear equations. This we have done with the results exhibited in Figs. 1a, 1b, and 1c.

For this purpose, we have used not only our own data, but also several sets of important data from the literature.

THE RELATION BETWEEN METABOLISM AND WEIGHT IN MATURE BIRDS OF DIFFERENT SPECIES

Fig. 1a represents the metabolism-weight relationship in birds obtained from papers by three investigators—Benedict and Fox, Gajja and Males, Terroine and Trautemann.

The data were plotted on a log-log grid. The rising curve represents the total metabolism; the declining curve represents metabolism per kilogram—both plotted against body weight. The metabolism per kilogram data are distinguished by cross-bars. The equation was fitted

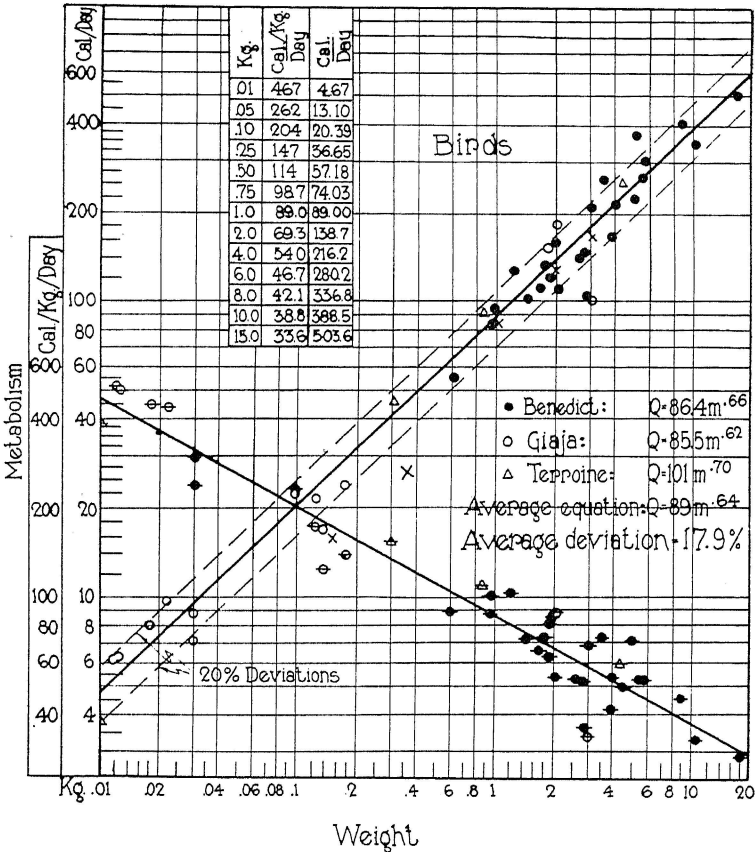


Fig. 1a.—A species comparison of metabolism of birds. The rising curve represents total metabolism per day; the declining curve represents metabolism per kilogram per day. The Calories per kilogram data points are distinguished from the total metabolism curves by cross-bars. The equations relating total metabolism with weight for each group, and also for all groups, are given on the chart. The equations were computed by the method of least squares. The broken lines represent 20% deviations. The x's, not included in the average lines, represent respectively, beginning with the lowest, Riddle's dove and pigeon and Mitchell's chickens at different weight levels.

(by the method of least squares) separately to each of these three sets of data, and also to all the three groups combined.

The values of the exponent (as shown on the chart) vary from 0.62 to 0.70; and the values of the coefficient vary from 85.5 to 101.0. The equation for all groups when combined is

$$Q = 89m^{.64}$$

or, for the declining curve, it is, of course,

$$Q / m = 89m^{-.36}$$

The broken curves represent ± 20 per cent deviations from the average. The percentage deviation of each observed value was computed from the corresponding equation value and the average of these deviations is 17.9 per cent from the average.

This deviation is not so great considering that the range in weights is from about .01 to about 20 kilograms—or 1 to 2000; that these measurements were made by three different investigators using quite different methods (Benedict and Fox used the Benedict “universal” apparatus, Giaja and Males used the “method of confinement”, Terroine and Trautemann used Haldane’s gravimetric method); with the exception of Terroine’s chicken and goose, the birds were not domesticated (they were “wild” birds). Forty-five different birds are included in this chart and equation.

After the equation was fitted to the data, we plotted in one (the “mature”) value for the dove, one for the pigeon (data by Riddle, Smith, and Benedict) and a little further up the values for Mitchell’s chicken data. All these extra values are represented by x’s. The dove is far below the average, as is also the pigeon, although Terroine’s pigeon is above the average line. Mitchell’s values for the chicken come quite close to the average.

THE RELATION BETWEEN METABOLISM AND WEIGHT IN MATURE MAMMALS OF DIFFERENT SPECIES

Fig. 1b represents the metabolism-weight relationship in mammals, using the weight-metabolism values as given in the preceding papers in this volume. Such body weights were included which are shown in Missouri Research Bulletin 101 to represent average “mature” weights. The exact weights used are given in Table 1. For the mouse (data by Aszodi) the average of three of his largest animals was used. In the case of the dog, two weights taken from Fig. 1a (Paper XXI) were included. The metabolism values for the corresponding weights were taken from the equations of the various species given in the preceding papers in this volume. The average metabolism of mature chickens based

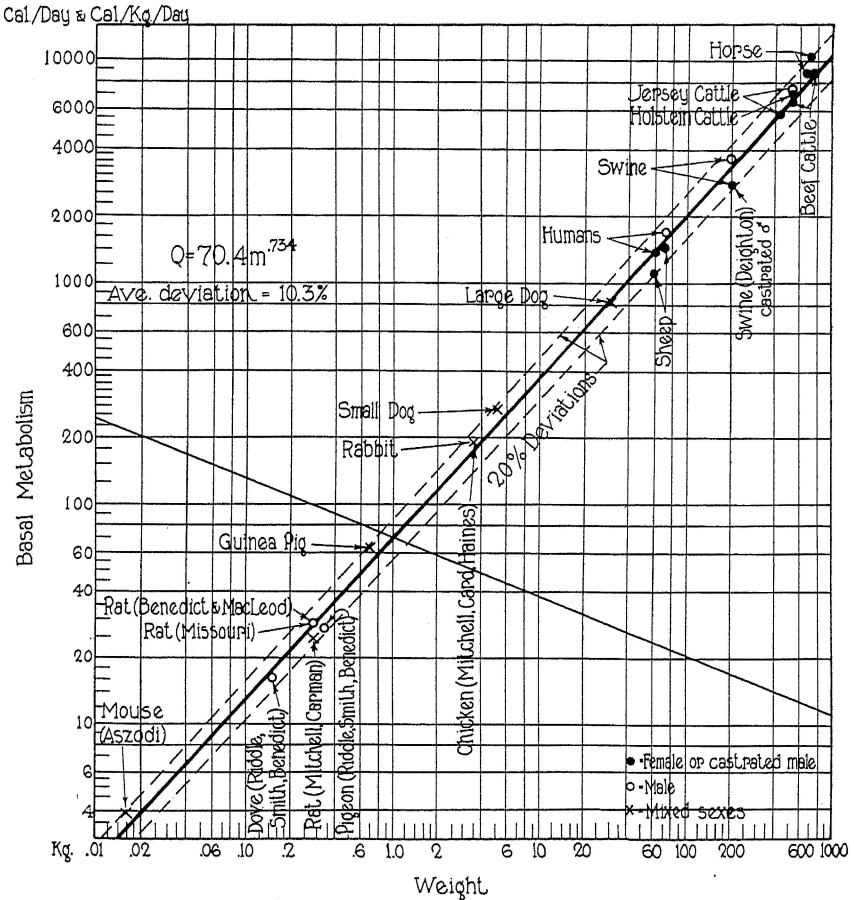


Fig. 1b.—A species comparison of metabolism of mammals, and also of the domestic fowl, pigeon, and dove. As in Fig. 1a, the rising curve represents total metabolism while the declining curve represents metabolism per kilo. The broken lines represent 20% deviations from the average. Note that unlike in Fig. 1a all points are within $\pm 20\%$ of the average, and that the equation for these animals is $Q = 70.4m^{.734}$ as compared to $Q = 89m^{.64}$ for the birds in Fig. 1a. With the exceptions noted, the data for horses, cattle, swine, sheep, rats, and chickens are Missouri data.

on Mitchell's chicken data was also included; it coincides with the average metabolism value of the mature rabbit.

As before, equation (3) was fitted by the method of least squares. The equation is

$$Q = 70.4m^{.734}$$

the values of the constants of which are, by the way, quite close to the

constants of Kleiber's "best" equations. Kleiber's "best" constants may be written in the form of equation

$$Q = 73.3m^{.74}$$

including his 13 animals, or

$$Q = 73.2m^{.73}$$

including his 9 animals.

It will be recalled that for birds (Fig. 1a) the equation is

$$Q = 89m^{.64}$$

Why should the bird data have a lower value for the exponent and a higher value for the coefficient than the mammal data?

The average percentage deviation for the mammal data, Fig. 1b, is 10.3 per cent as compared to the bird data of 17.9 per cent. The weight range is from about .02 to about 1000 kilos, or 2 in 100,000.

Note that among domestic animals swine have the lowest metabolism; then come sheep. Horses and Cattle have the highest metabolism.

TABLE 1:—COMPARISON BETWEEN OBSERVED AND COMPUTED METABOLISM VALUES FOR DIFFERENT ANIMALS.

Species, Breed & Sex	Mature Wt. Kgs.	Observed Values Cal./dav	Mammals Only Q = 70.4m ^{.734} Av. Dev. = 10.3%		Combined Mammals & Birds Q = 86.5m ^{.695} Ave. Dev. = 18.6%		Author
			Computed Values Cal./day	% Dev.	Computed Values Cal./day	% Dev.	
Horse Females	675	10826	8400	+28.9	7501	+44.3	Missouri
Horse Geldings	650	9098	8171	+11.3	7309	+24.5	Missouri
Beef Steers	700	8910	8627	+3.3	7690	+15.9	Missouri
Beef Females	500	6600	6739	-2.1	6107	+8.1	Missouri
Holstein Fems.	500	7210	6739	+7.0	6107	+18.1	Missouri
Jersey Males	500	7307	6739	+8.4	6107	+19.7	Missouri
Jersey Females	420	5865	5930	-1.1	5419	+8.2	Missouri
Swine Males	200	2780	3440	-6.4	3260	+12.3	Missouri
Swine Females	200	2780	3440	-19.2	3260	-14.7	Missouri
Swine Barrows	200	2760	3440	-19.8	3260	-15.3	Deighton
Sheep Wethers	70	1440	1592	-9.5	1585	-9.1	Missouri
Sheep Females	60	1135	1421	-20.1	1429	-20.6	Missouri
Human Males	70	1700	1593	+6.8	1585	+7.3	Benedict
Human Fems.	60	1370	1421	-3.6	1429	-4.1	Benedict
Dog (mixed)	30	807	855	-5.6	889	-9.3	Lusk, Kunde
Dog (mixed)	5	266	229	+16.1	261	+2.1	
Rabbit (mixed)	3.5	189	177	+6.8	204	-7.4	Various
Guinea Pig (mixed)	.7	63.7	54	+17.5	67.5	-5.9	Various
Rat Males	.3	28.9	28	+1.8	37.0	-21.9	Missouri
Rat Males	.3	28.1	28	-1.1	37.0	-24.0	Missouri
Rat (mixed)	.3	24.7	28	-13.0	37.0	-33.2	Mitchell
Mouse (mixed)	.02	3.95	3.4	+16.9	5.1	-22.6	Aszodi

TABLE 1 (CONTINUED).—COMPARISON BETWEEN OBSERVED AND COMPUTED METABOLISM VALUES FOR DIFFERENT ANIMALS

Species, Breed & Sex	Mature Wt. Kgs.	Observed Values Cal./day	Birds Only Q = 89m. ⁶⁴ Ave. Dev. = 17.9%		Combined Mammals & Birds Q = 86.5m. ⁶⁵ Ave. Dev. = 18.6%		Author
			Computed Values Cal./day	% Dev.	Computed Values Cal./day	% Dev.	
Cassowary	17.6	516	558	-7.5	617	-16.3	Benedict
Condor	10.3	351	396	-11.4	428	-18.0	Benedict
Swan	8.9	418	360	+16.1	386	+8.3	Benedict
Javan Adjut.	5.7	307	271	+13.3	385	+7.6	Benedict
Jabiru	5.5	272	264	+3.0	271	+0.5	Benedict
Pelican	5.1	375	252	+48.8	264	+42.2	Benedict
Vulture	5.1	228	251	-9.2	263	-13.3	Benedict
Crane	4.0	220	217	+1.4	225	-2.1	Benedict
Crane	3.9	168	212	-20.7	219	-23.4	Benedict
Pelican	3.5	264	199	+32.7	204	+29.1	Benedict
Flamingo	3.1	215	181	+18.8	185	+16.1	Benedict
Eagle	2.9	106	174	-39.1	178	-40.3	Benedict
Curassow	2.8	149	172	-13.4	175	-14.9	Benedict
Screamer	2.6	142	165	-13.9	167	-15.1	Benedict
Guan	2.1	112	141	-20.6	141	-20.5	Benedict
Heron	1.9	162	136	+19.1	136	+19.4	Benedict
Heron	1.9	121	133	-9.0	133	-9.2	Benedict
Heron	1.8	134	129	+3.9	129	+4.0	Benedict
Heron	1.7	113	124	-8.9	123	-8.4	Benedict
Duck	2.1	187	141	+32.5	142	+32.0	Giaja
Duck	1.9	162	135	+20.0	135	+20.0	Giaja
Duck	1.9	157	133	+18.4	133	+18.5	Giaja
Eagle	3.0	102	180	-43.1	184	-44.3	Giaja
Owl	1.5	108	113	-4.4	112	-3.2	Benedict
Gull	1.2	127	101	+25.7	99	+28.8	Benedict
Skua	1.0	98	87	+12.6	85	+15.7	Benedict
Ibis	.9	85	86	-1.2	83	+2.5	Benedict
Bittern	.6	56	64	-12.5	61	-8.0	Benedict
Chicken Mixed	3.5	187	198	-5.6	204	+8.3	Mitchell
Chicken	.9	94	81	+17.0	78	+21.2	Terroine
Goose	4.3	262	228	+14.5	237	+10.3	Terroine
Pigeon	.3	47	41	+13.6	38	+23.5	Terroine
Pigeon	.3	27	45	-39.0	41	-34.1	Riddle
Dove	.2	16	26	-39.0	24	-31.8	Riddle
Turtle Dove	.2	25	29	-15.6	26	-5.8	Giaja
Turtle Dove	.13	22	24	-7.4	21	+4.6	Giaja
Falcon	.14	17	25	-31.0	22	-22.3	Giaja
Quail	.1	23	20	+14.0	18	+30.4	Giaja
Love Bird	.03	7	9	-23.4	8	-7.8	Giaja
Sparrow	.03	9	9	-5.4	8	+14.0	Giaja
Finch	.02	10	8	+26.4	6	+54.7	Giaja
Finch	.01	6	5	+16.9	4	+46.5	Giaja
Finch	.01	6	5	+18.5	4	+48.8	Giaja
Widow Bird	.01	4	5	-18.0	4	+3.8	Terroine
Swallow	.02	8	7	+19.3	6	+46.9	Giaja

THE RELATION BETWEEN METABOLISM AND WEIGHT OF ALL MATURE ANIMALS (MAMMALS AND BIRDS COMBINED)

Fig. 1c represents both mammals and birds combined on one chart and in one equation.

As before, the equation was fitted by the method of least squares, ± 20 per cent deviation lines were drawn, the average percentage deviation was computed, and the results are all lettered in on the chart.

The equation is seen to be

$$Q = 86.5m^{.685}$$

The average deviation is 18.6 per cent.

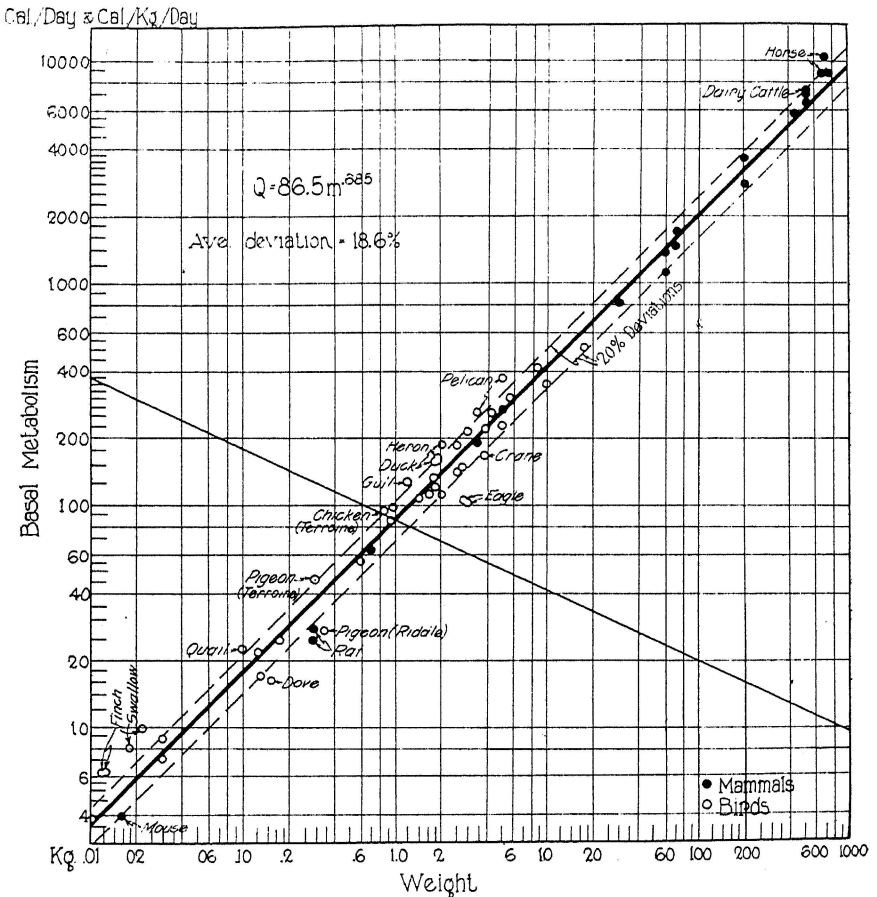


Fig. 1c.—A species comparison including all the mammals and birds given in Figs. 1a and 1b. The equation for all species is $Q = 86.5m^{.685}$. The broken lines represent 20% deviations. Only the data points which are 20%, or more, removed from the average are labelled; the others are within $\pm 20\%$ of the average. The declining curve represents Calories per kilogram per day.

The range is from 10 grams to 1,000,000 grams—the relative range being 1 in 100,000.

The names of the species, the metabolism of which are 20 per cent or more from the average line, are indicated on the chart. As before, the metabolism values for Riddle's doves and pigeons are far below the equation average, while Terroine's pigeon (also chicken and duck) metabolism values, are above the average. The rat and mouse metabolism values are likewise below the average line, while the metabolism values of cattle and horses are above the average line. It will be recalled, however, that the metabolism data of the horses are not strictly basal as the horses were measured in standing position, and it was not possible to keep them absolutely quiet.

While there may be a systematic deviation from the average (large animals having a higher metabolism than is indicated by the general trend, and small animals having a smaller metabolism than is indicated by the general trend) as is maintained by Benedict and apparently also by Kleiber, an analysis of relative deviations in different regions of the curve in Fig. 1c does not show this, and we shall perhaps not know it definitely until all species are measured under strictly identical conditions. Whatever the uncertainties as regards fine details, it is remarkable that an average curve representing a weight range of 1 to 100,000 including over 50 different species of mammals and birds measured by different men in different countries under different conditions should agree with observed values as well as it does.

The exponent in the metabolism-weight relation in Fig. 1c being not far from $\frac{2}{3}$, the surface area partisans will probably see in this a substantiation of the "surface law". But whatever the theoretical explanation and quite independent of whatever it may be, it does seem more convenient to express metabolism in relation to weight raised to an appropriate power rather than to area.

THE RELATION OF METABOLISM DURING GROWTH WITHIN GIVEN SPECIES TO THE GENERAL CURVE OF METABOLISM OF MATURE ANIMALS OF DIFFERENT SPECIES

Fig. 1d represents the mammals metabolism curve from Fig. 1b (fine broken curve), and also the metabolism-weight relationships for the several species during growth (heavy continuous curves). The rising curve represents total metabolism per day. The declining curve represents Calories per kilo per day. It is clear that at given weights the metabolism of the young animals is usually higher than the level of the general curve.

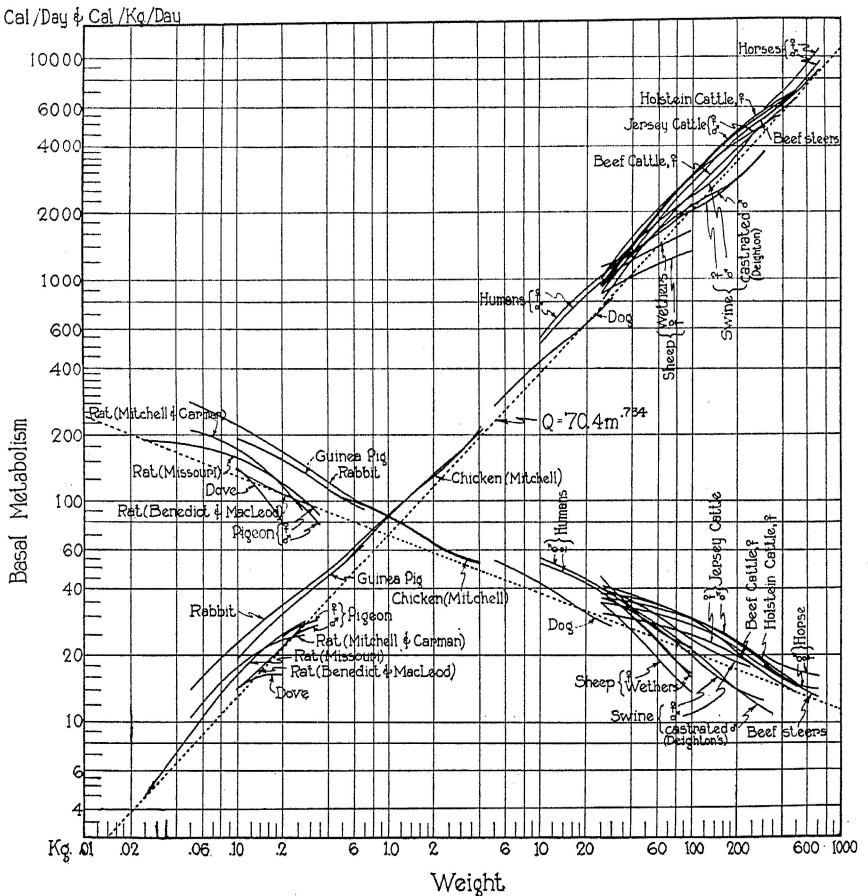


Fig. 1d.—The relation of individual weight curves of basal metabolism during growth to the general curve for mature animals given in Fig. 1b. Note that the curves of metabolism during growth do not always coincide, or even run parallel, to the general curve for mature animals. The rising broken line represents total metabolism per day of equation $Q = 70.4m^{0.754}$; the declining broken line represents metabolism per kilo per day of the equation $Q/m = 70.4m^{-0.286}$.

A COMPARISON OF THE DECLINES IN METABOLISM PER UNIT WEIGHT WITH INCREASING WEIGHT DURING ACTIVE GROWTH IN DIFFERENT SPECIES AS PLOTTED ON AN ARITHLOG GRID

Fig. 1e represents the metabolism-weight relationships in the different species of the actively growing animals previously discussed; it also gives a table of numerical values for metabolism at appropriately spaced body weights.

It is difficult to interpret a chart of this sort no matter how inherently interesting the facts may be. The reason for the difficulty is that at given weights the different species are in different developmental stages. At weight of 70 kilograms, for example, sheep and man have the same metabolism because they not only have the same body weight, but they are also in the same developmental stage. But cattle at this weight have a much higher metabolism because 70-kilo cattle are physiologically much younger than man or sheep. It is clear that the younger the animal is physiologically, the higher is its metabolism per unit weight; and also the smaller the animal, the higher is its metabolism per unit weight. Weight and physiological age thus influence, independently and in opposite directions, the metabolic rate, and rational comparisons are difficult unless it is possible to correct for each of these independent factors separately.

SUMMARY AND CONCLUSIONS

1. The basal metabolism of mature mammals and of the domestic fowl, increase directly with the 0.734 power of body weight. The metabolism per unit weight raised to the 0.734 power is 70.4. That is, the equation relating metabolism, Q , to weight, m , is

$$Q = 70.4m^{.734}$$

Among domestic animals swine have the lowest, cattle and horses the highest relative metabolism.

2. For "wild" birds, the metabolism increases directly with the 0.64 power of weight, and the metabolism per unit weight raised to the 0.64 power is 89. That is, the equation is

$$Q = 89m^{.64}$$

3. If the data of all the mammals and all the birds are combined, then, statistically, the metabolism varies with the 0.685 power of weight, and the metabolism per unit weight raised to the 0.685 power is 86.5. That is, the equation is

$$Q = 86.5m^{.685}$$

4. The average percentage deviations from the averages are respectively 10.3 for the equation for mammals; 17.9 for the equation of wild birds; 18.6 for the combined bird and mammal equation.

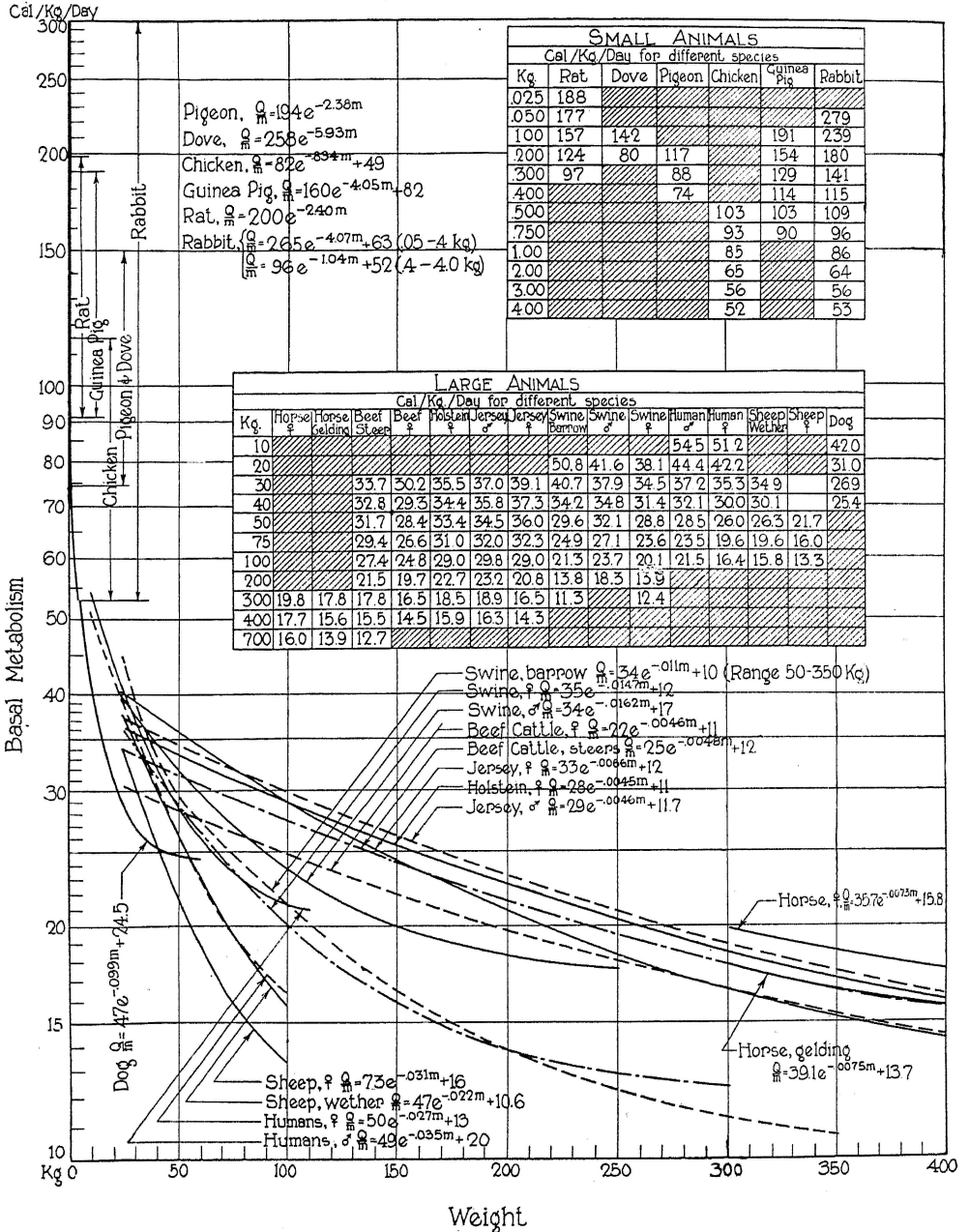


Fig. 1e.—A comparison of the decline in metabolism per unit weight with increasing weight, during active growth, in different species, plotted on an arithlog grid.

5. There is no doubt but that it is more reasonable to relate metabolism of *mature* animals of different species to their weights raised to some power than to area. This is no argument against the theoretical implications of the surface area theory; it is an argument only against attempting the very difficult, if not the impossible task, of evaluating surface areas of different species of animals when metabolism could be easily related to, say, the $\frac{2}{3}$ power of weight which is theoretically, and probably practically, equivalent to relating metabolism to area. At any rate, the agreement between observed and computed values may be made as good by relating metabolism to weight raised to an appropriate power, as to area.

6. The question as to the exact value of the power to which the weight should be raised to be used as unit of reference for metabolism can not at present be answered. All one can say now is that the value of the true power lies between the limits of 0.64 and 0.74. More, and better, basal metabolism data are needed to give a final answer to this question. In the meantime, a tentative "standard" may be adopted, such as one of the curves given in this paper (Figs. 1a to 1d).

7. The metabolism-weight relationship during growth is different from such a relationship in mature animals of different species; the former relationship is exponential as explained in the preceding papers of this volume, while the latter is logarithmic.

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