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GROWTH AND DEVELOPMENT

With Special Reference to Domestic Animals

XXIV. The Decline in Energy Metabolism Per Unit Weight With Increasing Age in Farm Animals, Laboratory Animals, and Humans.

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*Division of Responsibility: A. C. Ragsdale, Feeding and Management of Dairy Cattle; E. A. Trowbridge, Feeding and Management of Beef Cattle, Sheep, Horses, and Swine; S. Brody and W. C. Hall, Metabolism Measurements; S. Brody, Preparation of Manuscript.

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 and J. E. Comfort.

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.

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

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GROWTH AND DEVELOPMENT

With Special Reference to Domestic Animals

XXIV. The Decline in Energy Metabolism Per Unit Weight With Increasing Age in Farm Animals, Laboratory Animals, and Humans.*

ABSTRACT

1. This bulletin presents data on *resting* and *basal* energy metabolism per unit weight as a function of age for dairy cattle, beef cattle, sheep, horses, and swine from birth until about $3\frac{1}{2}$ years of age; also *basal* metabolism data for white rats grown under various conditions of food supply, especially when the food was limited so that the live weight of the immature animals remained constant.

2. These data, presented mainly in graphical forms, are analyzed mathematically, and in the case of normally fed animals, shown to follow the age curve represented by the equation $Q/m = Ae^{-kt} + C$ in which Q is the heat production for weight m , and age t . The constant C in the equation may be dispensed with when representing brief segments of the age curve, or when confining the data to the period of senescence. These equations were also fitted to published data, and, where possible, compared to our data for the same and for different species.

3. Interpretative discussions are presented regarding the factors shaping the entire life curve of metabolism per unit weight; the probable relative influence of the visceral organs, surface area, and live weight on the basal metabolic rates; the relative influences of body weight, age, and relative physiological maturity on the metabolic rate; species comparisons of age changes in metabolic rates; and units of reference for metabolic rates.

4. Published data on the age changes in basal metabolism of humans and pigeons are analyzed mathematically, especially as they relate to the period of senescence. It is shown that there is a slight but unmistakable decline in metabolism per unit weight with increasing age during the period of senescence.

5. Gestation increases the metabolism per unit weight; lactation increases this still further. There are marked seasonal variations in the metabolism per unit weight in sheep with the peak occurring in spring and the trough in late autumn.

I. INTRODUCTION

This paper is an extension of Missouri Agricultural Experiment Station Research Bulletin 166. There, the energy metabolism per unit weight during growth was expressed as a function of body weight; here, the energy metabolism per unit weight is expressed as a function of age.

1. **The General Age Curve of Metabolism:**—There is at least one species, the domestic fowl, for which energy metabolism data are available for both prenatal and postnatal life. On the basis of these data we have prepared a "life curve" of metabolism for this species. This is shown, in somewhat diagrammatic form, in Fig 1a, both with reference to increase in body weight as well as to increase in age.

The metabolism per kilo is seen to decline at an ever decreasing rate from about 2000 Calories at incubation age of 4 days to about 100 Calories at hatching age. Following hatching, it rises to nearly 200 Calories during the third week, when a postnatal maximum is attained.

*Paper No. 51 in the Herman Frasch Foundation Series.

The decline following this maximum is uneventful, approaching, apparently, about 50 Calories per kilo as limit, at least in the larger breeds of chickens.

The life curve of the domestic fowl, shown in Fig. 1a, is perhaps typical of the life curves of all other species of farm animals. They all certainly show a rise in metabolism in the early postnatal stages of growth. However, in comparison with the entire curve, the rise is not very striking.

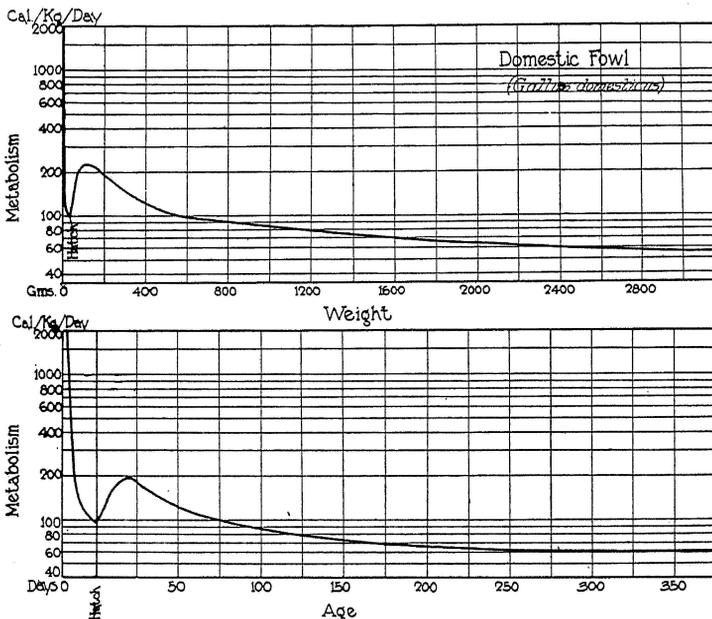


Fig. 1a.—A diagrammatic representation of the age curve of metabolism of the domestic fowl. The prenatal segment represents average of published data. See Needham for the literature on the metabolism of the chick embryo. The postnatal segment represents the average of Mitchell's and our data on the metabolism of chickens.

2. Possible Causative Factors Moulding the Shape of the Age Curve of Metabolism:—What might be the causes of the peculiar shape of this curve? The following possibilities suggest themselves.

a. During the prenatal period of growth, the life processes are nearly altogether vegetative. The organism is in a nearly constant aqueous environment; the nervous and muscular systems are practically inert, all voluntary movements and all sensory stimuli being absent. On hatching, the organism is exposed to a new—a terrestrial—environment filled with numerous stimuli to which the nervous and muscular systems react, with consequent expenditure of energy. This may explain the abrupt postnatal rise in energy expenditure. This rise may

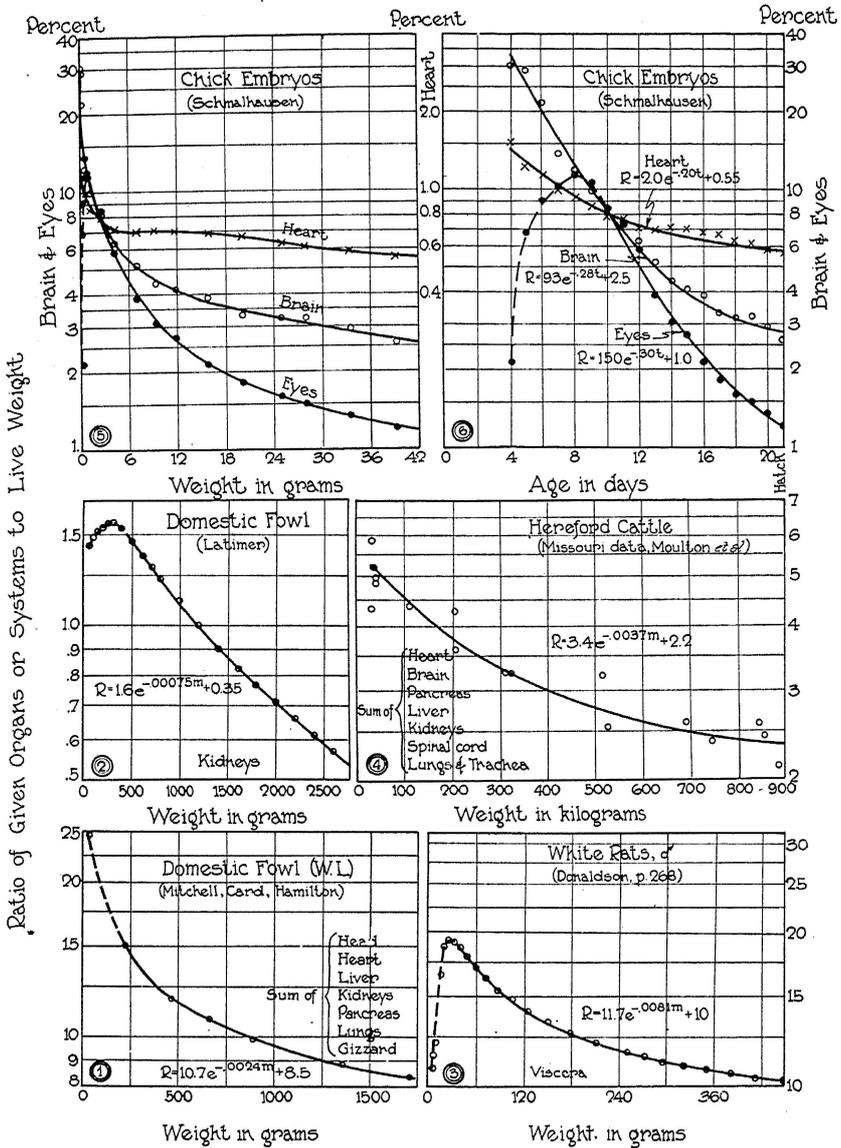


Fig. 1b.—Age changes of certain organs and organ systems, with respect to live weight. The data points represent the percentages that several of the organs or systems bear to live weight, while the curves represent equation 2b fitted to the data. In the equations on the charts, R represents the percentage ratios of each of the indicated organs or systems to live weight. The broken segments represent parts of the curve to which the equation 2b does not fit. Charts (5) and (6) represent the ratios for the given system in the chick embryo, the ratios in (5) being plotted against body weight, while in (6), against age. The purpose of this chart is to show that the relation of some visceral organs to live weight tends to be the same as the relation of metabolism to body weight.

continue with the increase in responsiveness of the nervous, endocrine, and muscular systems to the environment until a certain maximum responsiveness and maximum metabolism per unit weight is attained.

b. The maximum energetic responsiveness of the organism (per unit of its body weight) to the environment is probably coincident with the maximum development (in mass, or area, or physiological function) of the vital organs in comparison to the total body size. That this seems to be the case is shown by the fact that the age curve (with respect to live weight) of the visceral organs of the body has the same general form as the age curve of metabolism with respect to live weight. By way of substantiation of this suggestion, a series of age curves for the relation between the mass of visceral organs and total body weight are shown in Fig. 1b. It has been previously shown (Fig. 1c) that in

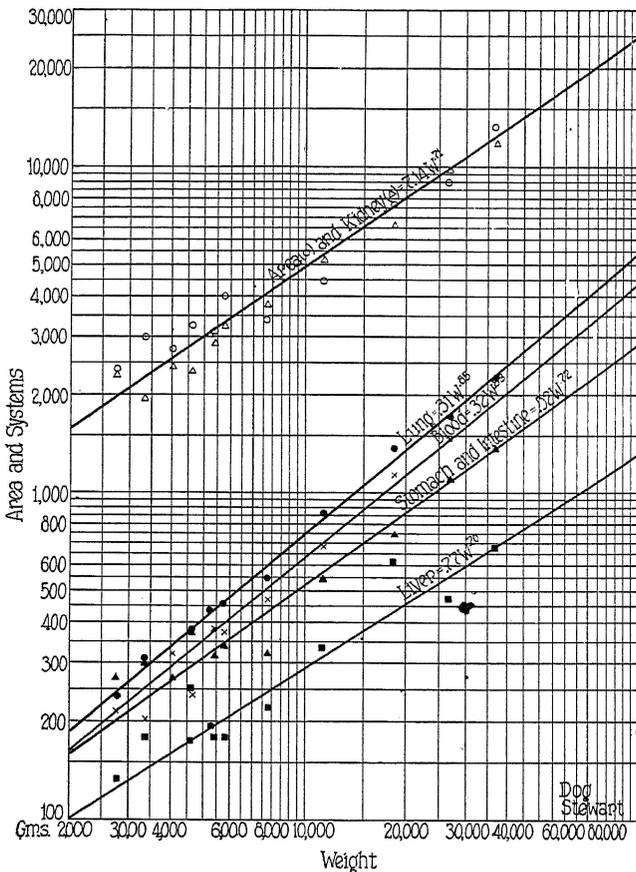


Fig. 1c.—This curve is the same as Fig. 6, p. 17, of Missouri Research Bulletin 115. It shows that within certain body weight limits, the course of increase in weight of some visceral organs with respect to body weight in the dog follow the same course as surface area.

dogs the weight of some visceral organs with respect to live weight follows the same course as does the surface area, which may explain the fact that metabolism follows the same course as does area in mature animals of different live weights.

Dr. John Hammond* has called our attention to the fact that one difference between the improved domestic breeds of animals and the wild stocks from which they originated is that the former animals have proportionately more flesh and less of visceral tissue than the latter. In this respect, the wild animals show greater resemblance to the young of their species than do the domestic animals. On the basis of these considerations, one would expect that wild animals or thin animals (which have a greater proportionate mass of visceral tissues) would have a higher metabolism than domesticated or fleshy animals. Recently published data by Benedict and Petrik on the basal metabolism of the wild rat shows, indeed, metabolic values which are 35 to 40% higher than those of the domesticated fleshy Albino rat. May not this difference between the metabolism of the Norway and Albino rats be explained by the greater relative mass of visceral organs in the former? Riddle, Smith, and Benedict have likewise found a much higher metabolism in a feral migratory species of dove reared in captivity than in the related non-migrating domestic doves and pigeons. These authors suggest this difference to be due to the relative differences in activity of the thyroids. We are inclined to attribute the higher metabolism in the "wild" breeds to relatively greater proportions of visceral organs than in the domesticated breeds.

c. The exceedingly high metabolism per unit weight in the early stages of life may be associated with the exceedingly rapid rate of growth. It is reasonable to assume with Terroine and Wurmser, Needham, Rapkine, and others, that energy is required for the growth process; it requires energy to raise the potential from the level of inanimate matter to that of living tissues; and, other conditions being the same, the higher the rate of growth, the greater, one might expect, would be the energy metabolism per unit weight and time.

Furthermore, the exceedingly rapid rate of growth in the early stages of growth is associated with a correspondingly rapid rate of absorption of nutrients (see Needham, Fig. 253, p. 932). "On the sixth day, for instance, the (chick) embryo absorbs its own mass of dry solid, which would be equivalent to an adult man eating about 150 pounds of food per day. During the time between the 6th and the 18th days of incubation, this rate falls to about a quarter of its original value." (Needham, p. 933.) In adults it is known that ingestion of food is followed by a considerable rise in heat production. A 25% rise above basal

*Personal communication.

metabolism due to feeding is not unusual. Little is known about the specific dynamic effect, or heat increment of feeding, in rapidly growing animals; but it is not unreasonable to assume that the phenomenon of specific dynamic effect is also present in the young organism, and the very high metabolism in the early stages may, in part, be the result of the enormous consumption of food at that time. The rapid decline in metabolism per unit weight or area with increasing age may be associated with the rapid decline in food consumption per unit of body weight.

d. In the later stages of life, following what may be termed as middle age, the decline of metabolism is associated with the process of senescence, as indicated in the case of humans in Fig. 8b, page 40 and of pigeons in Fig. 9, page 45.

The above discussion assumes that under condition of basal metabolism (in a neutral thermal environment) surface area is not a *limiting* and not an important contributing factor to the intensity of energy metabolism. Surface area would, of course, become an important factor in case of deviation from a thermally neutral environment.

3. Mathematical Representation of the Age Curve of Metabolism;— During active growth obviously as the animal gets older it also grows heavier. It is therefore reasonable to assume that the course of metabolism per unit weight with increasing *age* during growth might be represented by the same mathematical function as was found to represent the course of metabolism per unit weight with increasing *weight* during growth. This idea appears to be correct in the main, and the chief purpose of the present bulletin is to present graphically and by means of equations the energy metabolism per unit weight as a function of age in the same manner as in Research Bulletin 166, where these same data were represented as a function of body weight.

The equations employed in Research Bulletin 166 were

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

and

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

in which Q/m is the heat production per unit weight with increasing weight, m . In equation 1a, k represents the relative, or when multiplied by 100 the percentage, decline in Q/m (heat production per unit weight) for an increase in one unit weight; e is the base of natural logarithms, and A is a parameter having the value Q/m when m is zero. Equation 2a assumes that the limiting value of Q/m is C ; that is, that under the given conditions of growth the value of Q/m does

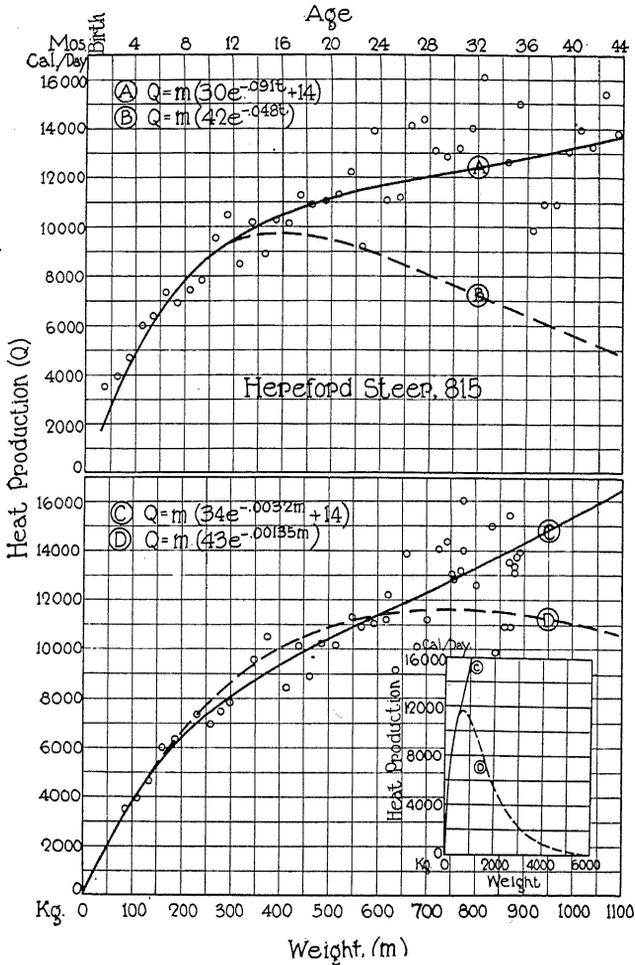


Fig. 1d.—Theoretical curves of the equations in the text fitted to the data (circles) of our steer 115. Curves D represent equation 1a; curves C represent equation 2a; curve A represents equation 2b; curve B represents 1b.

not, for practical purposes, fall below C. The numerical values of A and k are, of course, different in equation (1). and (2).

In this bulletin, we propose to use the same equations; but instead of having weight, m, in the exponent, we shall have age, t, that is

$$Q/m = Ae^{-kt} \tag{1b}$$

and

$$Q/m = Ae^{-kt} + C \tag{2b}$$

thus changing from Q/m as a function of m (weight) to Q/m as a function of t (age).

Equations (1a) and (2a) may, of course, be written, respectively, in the forms of

$$Q = mAe^{-km} \quad (1c)$$

and

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

and (1b) and (2b) may be written respectively as

$$Q = mAe^{-kt} \quad (1d)$$

and

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

Equations (1c) and (2c) on differentiation may be shown to have an inflection when $m = 2/k$, and (1c) has a maximum when $m = 1/k$.

On plotting Q (heat production per day) against m (body weight), one obtains respectively (for our steer 815) curves (D) and (C) in Fig. 1d. The same curves are shown in the inset, on a greatly extended scale, respectively by curves (D) and (C). The Q/m vs m curves for equations (1) and (2) for this steer are shown on page 15 of the preceding report (Research Bulletin 166).

Now since the total metabolism (Q) can not possibly decrease with increasing weight, therefore equation (1c) and also equation (1a), from which (1c) is derived, can not represent the data for steer 815 beyond body weight of about 600 kilograms; or in general, they can not represent the data beyond a certain limit. Hence, the necessity of having the constant C as indicated in equations (2b) and (2c). To be sure, equation (2c) also has an inflection in its curve, which inflection is perhaps without foundation in biological fact, and from this point of view equations (2b) and (2c) are not altogether satisfactory. Practically, however, this inflection is insignificant and causes no material deviation from the data in the particular region.

As previously indicated, if one represents the Q/m ratios by R and P , then one obtains from equations (1a) and (2a) respectively

$$\begin{aligned} R &= Ae^{-km} & (1g) \\ dR/dm &= -kAe^{-km} \\ &= -kR \end{aligned}$$

and

$$\begin{aligned} P &= Be^{-km} + C & (2g) \\ dP/dm &= -kB e^{-km} \\ &= -k(P - C). \end{aligned}$$

These forms bring out the similarity between the equations here used 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 "active mass", as well as between changes in the course of metabolism with changes in the rates of growth and rates of senescence as explained fully in Research Bulletins 97 and 105.

These ideas are likewise applicable to equations (1d) and (2d) relating Q (total heat production per day) to t (age) instead of to m (weight).

The following are the detailed procedures for locating the inflections and maxima in equations (1c) and (2c):

$$\begin{aligned} \text{For (1c) we have } Q &= mAe^{-km} \\ dQ/dm &= -mkAe^{-km} + Ae^{-km} \\ &= Ae^{-km}(1 - km). \end{aligned}$$

$$\text{On equating to 0, and solving for } m, \text{ we obtain} \\ m = 1/k$$

which is the weight at the maximum.

To obtain the inflection, the second derivative is obtained, equated to 0, and solved for m , as follows:

$$\begin{aligned} d^2Q/dm^2 &= Ae^{-km}(-k) - kAe^{-km}(1 - km) \\ &= Ae^{-km}(-k - k(1 - km)) \\ &= Ae^{-km}(k^2m - 2k) \\ k^2m &= 2k \\ m &= 2k/k^2 = 2/k. \end{aligned}$$

For (2c) we have:

$$\begin{aligned} Q &= m(Ae^{-km} + C) \\ dQ/dm &= m(-kAe^{-km}) + (Ae^{-km} + C) \\ &= Ae^{-km}(1 - km) + C \\ d^2Q/dm^2 &= -kAe^{-km} - kAe^{-km}(1 - km) \\ &= Ae^{-km}(-k - k(1 - km)) \\ &= Ae^{-km}(mk^2 - 2k) \\ m &= 2/k \text{ which is the inflection.} \end{aligned}$$

The equation has no maximum for practical purposes.

II. FARM ANIMALS

1. Dairy and Beef Cattle

a. Definitions and Conditions of Resting and Basal Metabolism.—

The data discussed in this section were already published (pp. 16 to 31, Missouri Research Bulletin 166), but as related to body weight rather than to age. The definitions of *resting* and *basal* metabolism were also given. *Resting* metabolism represents the heat production of the animals while they are in the natural lying position taken just before the morning feeding, and therein do our *resting* metabolism data differ from our *basal* metabolism data. Resting metabolism is basal metabolism plus the heat increment of feeding, just before the morning feeding.

The condition of *resting* metabolism as thus defined is not very satisfactory for the reason that the actual value of this metabolism varies with the amount and nature of the diet. It is true only for the animals as fed by us; that is, for animals as fed and managed according to good commercial herd practice in Missouri. The resting metabolism values would be higher for animals fed more liberally, and lower for animals fed less liberally.

A few words are called for on the possible error introduced in our metabolism values by ignoring the methane production in cattle.

It is generally known that there is fermentation in the digestive tract of ruminants. The products of the fermentation are carbon dioxide and methane. The fermentation process is, we take it, anaerobic, so that no oxygen is used for this process; and, therefore, the oxygen consumption is not influenced thereby. As the metabolism data here presented are based exclusively on oxygen consumption, therefore the carbon dioxide produced during fermentation is of no concern to us for the present purpose.

But what about the methane? As this is not a product of metabolism of the animal (it is a product of bacterial origin), we have no direct interest in it. However, since methane is not absorbed in the soda lime, and since the rate of oxygen consumption is measured volumetrically, in the closed-circuit system, the reading for oxygen consumption will be less by the amount of methane that may accumulate in the system, and thus result in an error in the metabolism measurement. The final apparent metabolism value will be less than it really is by the amount of methane accumulated in the system. How large is this error?

In the writer's opinion, this error is insignificant; at least it is less than the experimental error inherent in measuring metabolism in general. This opinion is based on the following considerations:

(1) The *total* methane carbon eliminated by cattle appears to be from 5 to 9 per cent of the *total* carbon-dioxide carbon eliminated (see Forbes, Braman, Kriss *et al*, J. Agric. Res., 1931, 43, p. 1019;

also page 41, vol. 40, 1930). When, therefore, the respiratory quotient is 1, then the apparent oxygen consumption would be from 5 to 9 per cent less than the real oxygen consumption. This error would be reduced on decreasing the respiratory quotient.

(2) The aforementioned values by Forbes and associates for methane production were obtained in a respiration chamber in which case the *total* methane excretion is determined. But the method used by us for measuring metabolism involves the connection of the animal's respiratory system only to the apparatus, so that only that part of the methane which is exhaled through the lungs (after absorption into the blood stream) is accumulated in our respiratory apparatus. A part of it also may be excreted by the way of the oesophagus, although this seems improbable to us as the animals keep their mouths closed while having the mask on. When, however, regurgitation of the gas does occur, it would have to be sudden—a change which would be abruptly registered on our graphic record of the spirometer volume, and which is necessarily discounted for by our graphic-slope method of computing metabolism. We compute the metabolism not by finding the actual decrease in volume of the oxygen spirometer in the given time, but by measuring the *slope* of the graphic record, and an abrupt change in the volume of the system does not affect the *slope* of the graphic record. It is felt, therefore, that the graphically uncorrected-for accumulation of methane in the system is quite negligible, and may be completely ignored. We hope in the near future to obtain quantitative data on methane excretion by our method of measuring metabolism and perhaps determine the relative amounts of this gas excreted by way of lungs, oesophagus, and rectum.

b. Resting Metabolism Curves of Cattle Populations.—These are represented in Fig. 2a by breed and sex. Each data point represents a monthly average value for a given animal. Each monthly average value is the average of from one to ten single measurements during the given month.

The heavy curve passing through the data points represents the average, which was obtained as follows: Equation 2b was fitted to the data for each individual animal separately. The constants A, k, and C of the individual equations were then averaged, and the heavy curve in Fig. 3a is the average equation of the individual equations as thus obtained by averaging the constants. The broken curves represent 10 and 20% deviations from the average curves.

An attempt was also made to fit to the data equation 1b (which does not have the constant C), with the result shown by the straight broken line passing through the data points. The fit of the equation is fair until 12 to 15 months of age, but it obviously does not fit after

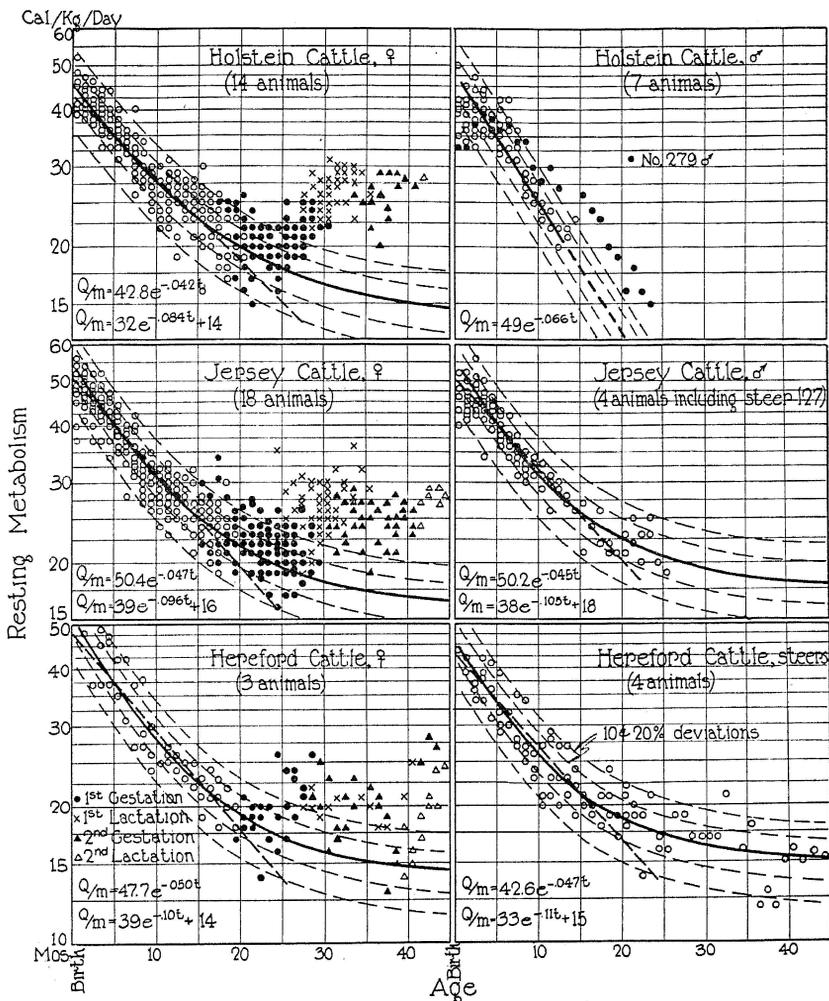


Fig. 2a.—Resting metabolism per unit live weight of our cattle populations as a function of age. The data points are monthly average values of individual animals. The heavy smooth curves represent equation 2b; straight, heavy, broken lines represent equation 2a; the light broken curves represent 10 and 20% deviation from the average. The meaning of each of the four symbols is indicated on the lower left corner of the chart. The curves represent data accumulated up to September 1, 1932.

this age. This is also shown by curve B in Fig. 1d. The constant C is an absolute necessity in the equation. But the fit of equation 1b is interesting in showing that until about 15 months the average decline in metabolism per unit weight in cattle is of the order of 4.8 per cent per month, as compared to a decline of about 9 per cent per year (or less than 0.8 per cent per month) between ages 1 and 5 years in humans

(see Fig. 8a). Does this difference in rate of decline in metabolism per unit weight with increasing age simply represent differences in declines in gains in weight, or does it represent differences in the rate of approach to physiological maturity? This problem is discussed in greater detail in connection with Fig. 11.

As in the preceding report, the gestation and lactation data are above the level of the average curve. We are as yet unprepared to interpret these results; we do not now know whether the high values during lactation are due to the additional food ingestion or to the energy expense of milk production. The problem of the energy expense of lactation distinct from food ingestion must be worked out in species, such as humans, dogs, rats, and swine, which have a simple digestive tract, which can be conveniently maintained on very simple diets, and which reach the post-absorptive condition within 12 to 15 hours

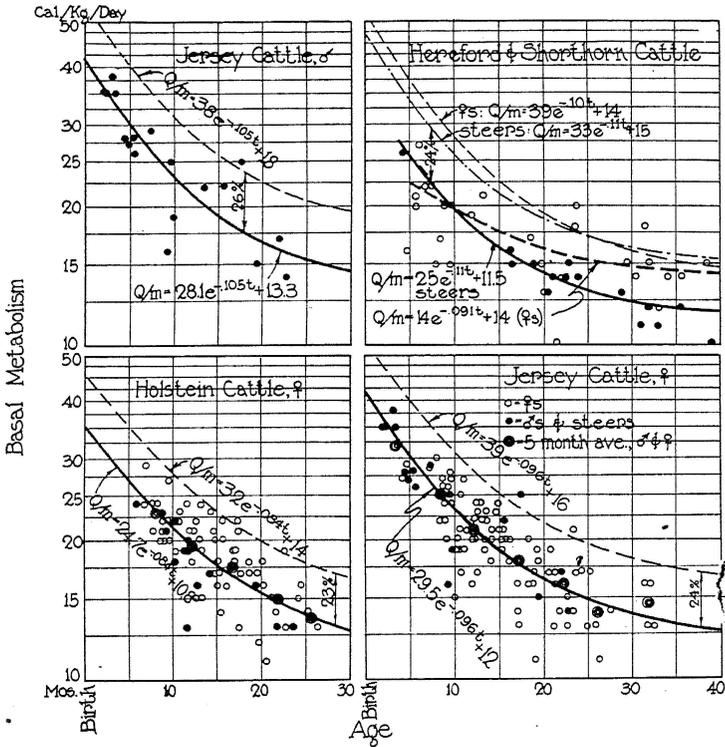


Fig. 2b.—Basal metabolism as a function of age in our cattle populations. The circles, etc., represent individual measurements. The heavy smooth curves represent the fit of equation 2b to the data. The broken curves represent the resting metabolism curves of Fig. 2a. The legend for each of the three kinds of symbols is given in the lower right quadrant. The average heat increments of feeding is seen to be between 23 and 26 per cent for dairy cattle during the whole period of growth. In the case of beef cattle, the heat increment of feeding seems to decrease with the age of the animals.

after feeding. It is obviously impracticable to fast heavily lactating cattle or sheep. We are at present collecting data on rats, humans, and swine for this purpose.

c. Basal Metabolism and Heat Increments of Feeding in the Cattle Populations.—Our *basal* metabolism data were obtained in the same manner as the *resting* metabolism data, except the animals were fasted 48 to 72 hours. As it is not practicable to subject to frequent fasts the very expensive animals at our disposal, and which according to our program must be managed under conditions of a commercial herd anyway, therefore our *basal* metabolism data are comparatively few—really too few for drawing general conclusions. But whatever data we have are presented in Fig. 2b. Each point represents an individual measurement. Data points representing individual measurements are naturally less reliable and more scattered on the chart than the points in Fig. 2a which represent averages of from one to 10 measurements.

The heavy smooth curve drawn through the data points in Fig. 2b represents equation 2b in the text; while the upper broken curve represents the *resting* metabolism of the groups, as traced from Fig. 2a. Note that the numerical values of the exponents are the same in both curves; that is, the slopes of both curves are the same, and the *percentage* differences between the two curves are the same for all regions of the curve.

The percentage difference between the curves represents, according to our definition, the average heat increments of feeding of the particular group of animals under observation. All this was discussed in detail in the preceding report (pp. 45 to 65, Missouri Research Bulletin. 166).

d. Resting Metabolism Curves of Individual Animals.—It was pointed out that equation 2b was fitted to the data of each individual animal separately. These data have been plotted, and they are exhibited in Figs. 2c to 2g. A very conspicuous feature of the curve of every lactating animal is the extraordinary high metabolic value during lactation. The lactation level of metabolism is seen to be between 30 and 60% above the general metabolic level in dairy cattle and 26 to 28% in beef cattle.

The average rise in metabolism due to lactation is indicated on each chart, showing conspicuous individual differences in this respect. While we have not as yet correlated the relative heights of the lactation levels of metabolism with the levels of milk yield and food ingestion, yet there is no doubt that such relations exist. However, the causative factor for the high metabolism during lactation may not be the process of lactation as such, but chiefly the heat increment of the extra food consumption during lactation. The decline in body weight of heavily lactating animals may be another contributing factor to the increase in metab-

olism per unit weight. This gross survey of the situation must necessarily be followed by an analysis of the partition of the heat production in relation to each of the various possible factors causing the high level of metabolism during lactation.

e. Individual Differences in Resting Metabolism.—What are the individual differences in energy metabolism? This is not only an important problem in biology, but it is evidently a problem of capital impor-

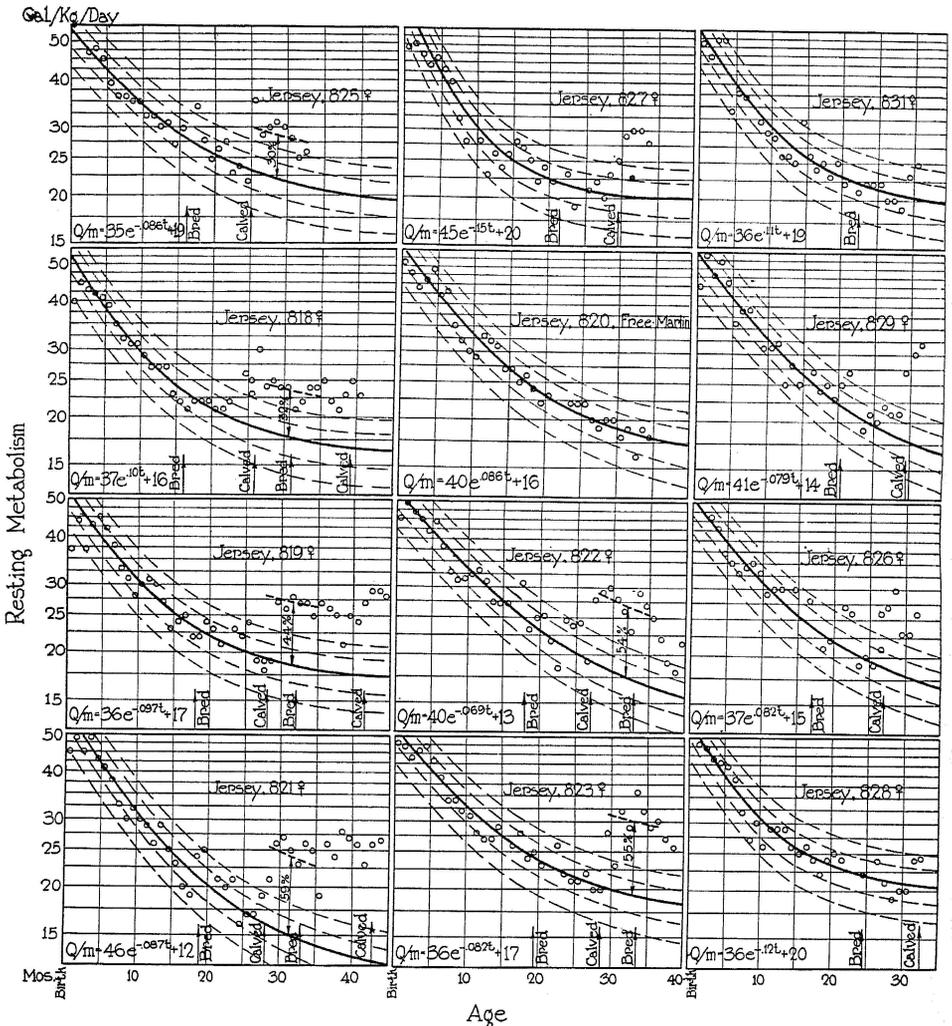


Fig. 2c.—Age curves of resting metabolism in Jersey cattle, females, of individual animals. The circles represent the observed monthly metabolism values. The heavy smooth curves represent equation 2b. The broken curves represent 10 and 20 % deviations from the average curves. The short, heavy, broken segments represent the average metabolism during lactation. The percentage differences between the lactation and general levels are indicated on the curves. The ages at breeding and calving are given.

tance in agricultural practice. The most important expense in animal or milk production is the cost of maintenance. Other conditions being the same, the smaller the cost of maintenance, the more efficient is the animal as a transformer of energy. There is a general belief among practical feeders of animals that there are "easy" and "hard" keepers; that is, that some animals can get along with less food and need less for maintenance than others. Are there really such differences between animals of the same breed? Are there breed differences in this respect?

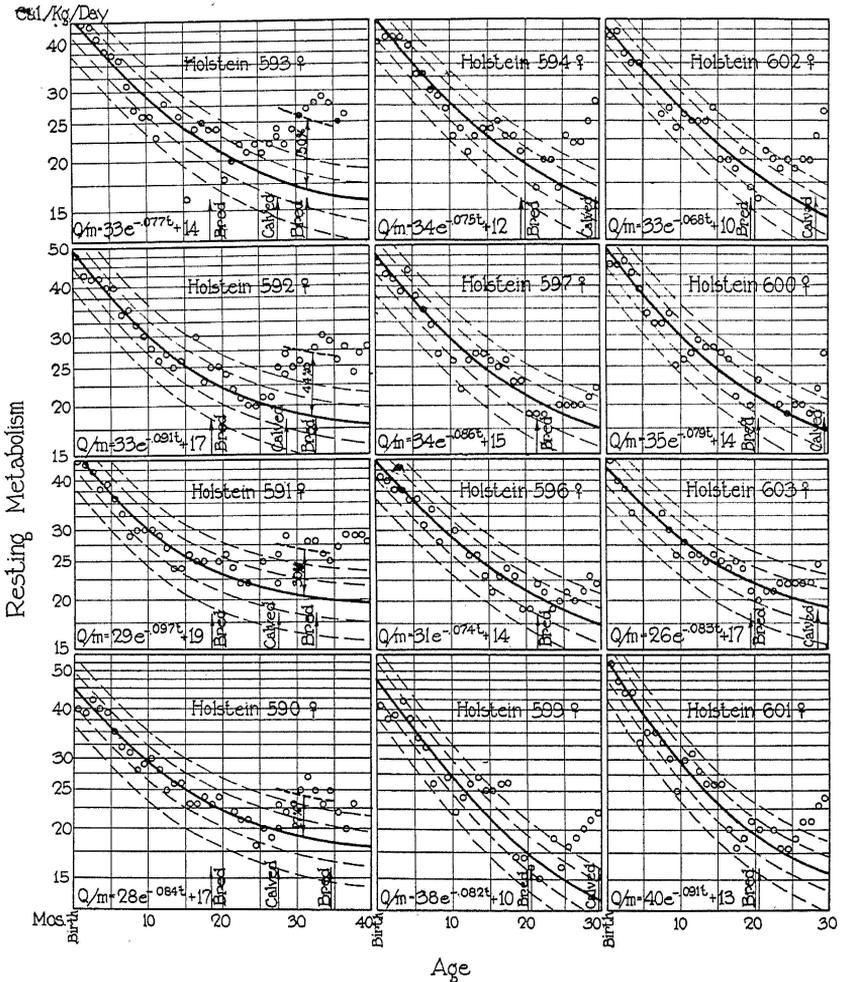


Fig. 2d.—Resting metabolism in Holstein cattle, females. See legend to Fig. 2c for additional explanations.

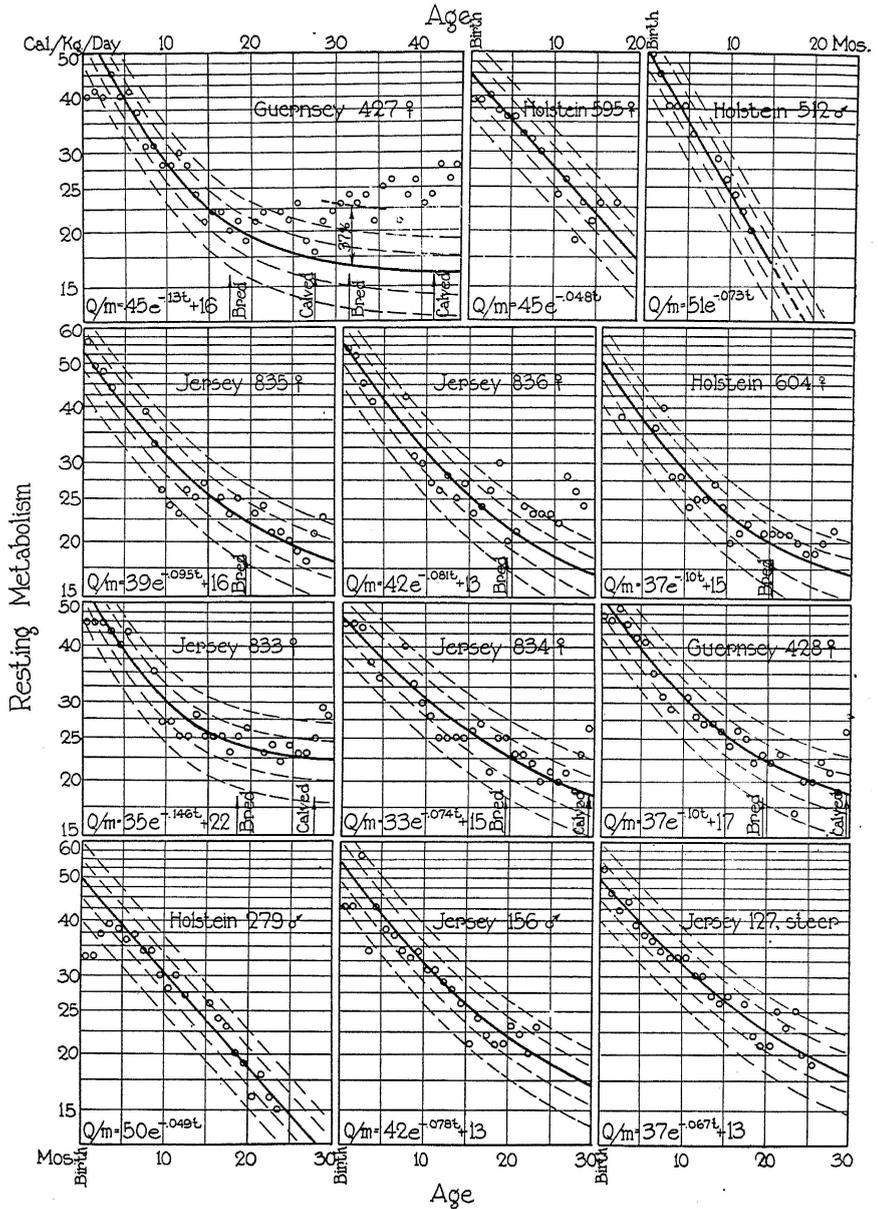


Fig. 2e.—Resting metabolism of dairy cattle, continued.

Are there species differences in this respect? Or, in general, do animals having approximately the same mature body weight and having the same rate of growth differ in their efficiency as transformers of energy? We shall refer again to these questions in connection with Fig. 8c comparing the age curves of metabolism of humans, white Americans and Australian Aborigines.

Fig. 2g represents a comparison of age curves of individual animals, and also of breeds. This comparison of individuals against *age* is less significant than a similar comparison of individuals against *weight*

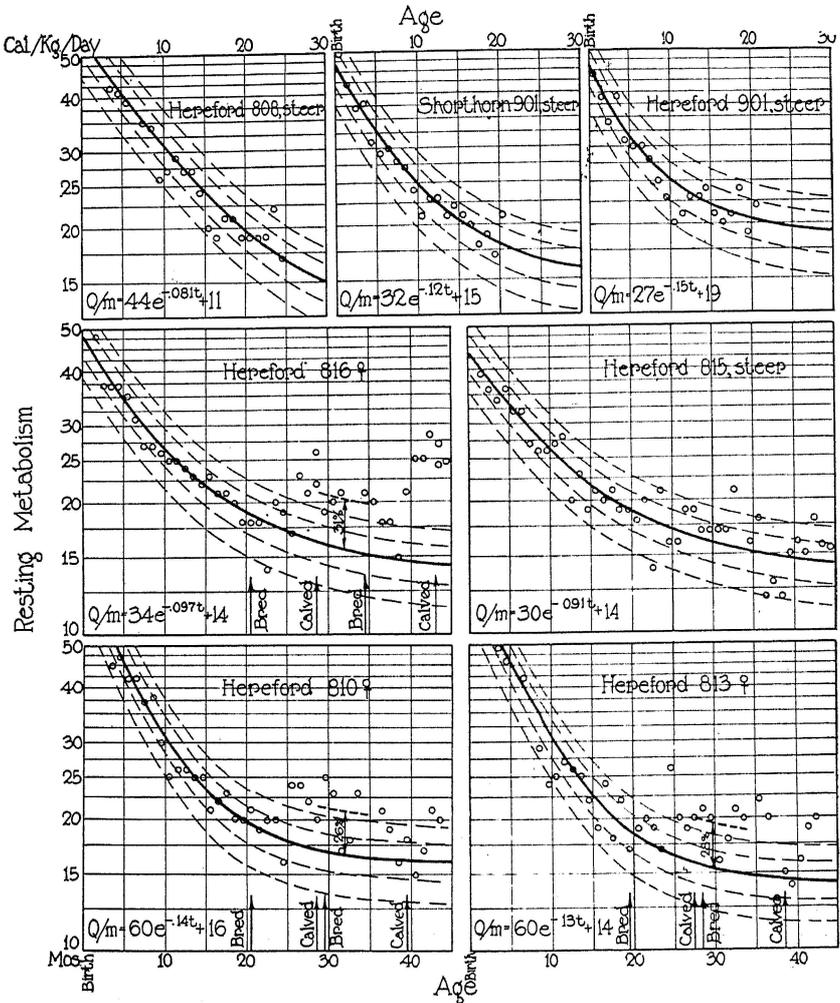


Fig. 2f.—Resting metabolism of individual beef animals. See legend to Fig. 2c for additional explanations.

given on page 31, Missouri Research Bulletin 166, because there are individual differences in body weight at given ages which affect the metabolism per unit weight. This comparison, as well as the one in the preceding report, suffers from the fact that the food intake was not controlled—the animals were merely fed according to the best practice of commercial herds—and so the metabolic rates might have been influenced by differences in individual food intake. We hope to report in the future on the relation between resting metabolism and food intake in these animals.

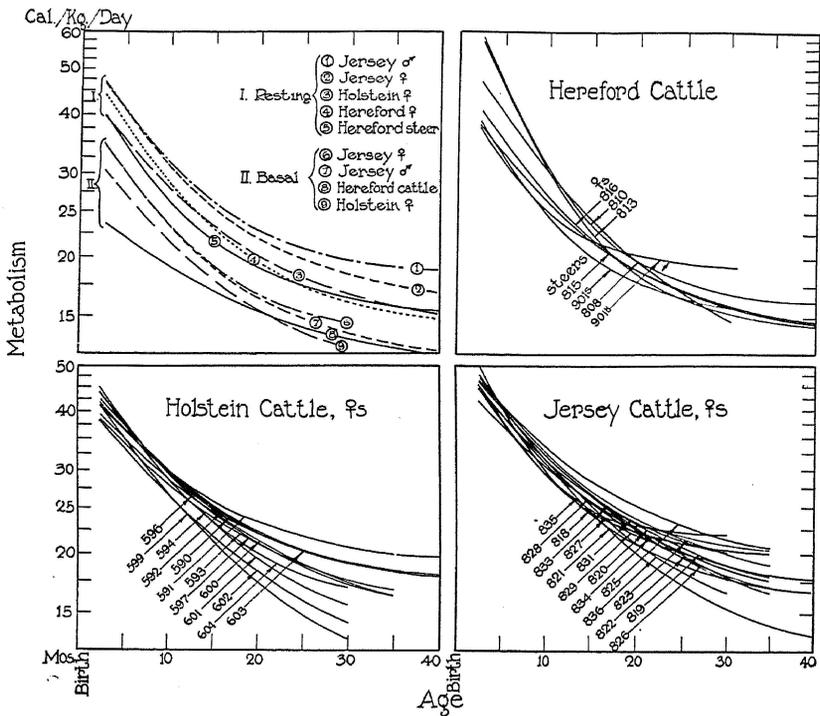


Fig. 2g.—Individual and breed differences in age curves of metabolism. The upper left quadrant represents curves of populations; the other quadrants represent individual animals with their herd numbers.

2. Sheep

With the exception of the complications arising from the peculiar wool covering of sheep, also the characteristic seasonal fluctuations in their sex lives, and the influence of pasture on sheep, the preceding discussions and explanations for cattle are applicable to sheep.

a. *Resting Metabolism of the Sheep Population and of Individuals.*—The population curve is shown in the lower left quadrant of Fig. 3a.

Fig. 3b represents individuals. The data on seven females are included. As before, each data point of resting metabolism represents a monthly average. The heavy smooth curve represents equation 2b, while the broken curves represent 10 and 20% deviations from the average curve. The lactation values were not included in the fitting of the equation to the data.

The most conspicuous characteristic of the population, as well as of the individual curves, is the cyclic variation in metabolic rate. What is the cause of this phenomenon?

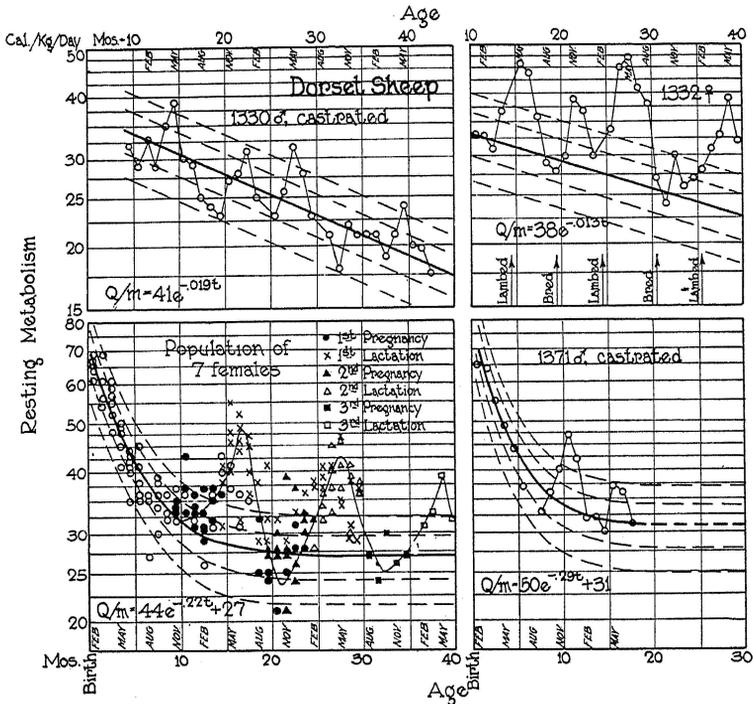


Fig. 3a.—Age curves of resting metabolism of sheep population (lower left quadrant) and of individuals.

Benedict and Ritzman have discussed many influencing factors in the metabolism of sheep. The recurrent gestations, lactations, shearings, seasonal changes in temperature, seasonal changes in food consumptions—both quality and quantity—are all important factors most of which have been discussed in the preceding report of this series, and in the preceding section as they relate to cattle.

The peak in the early spring coincides with the spring shearing, also with the last stages of gestation, and with the heavy lactation. There is also a change in the nature of the diet and in environmental temperature. As all these events come at nearly the same time, it is not possible

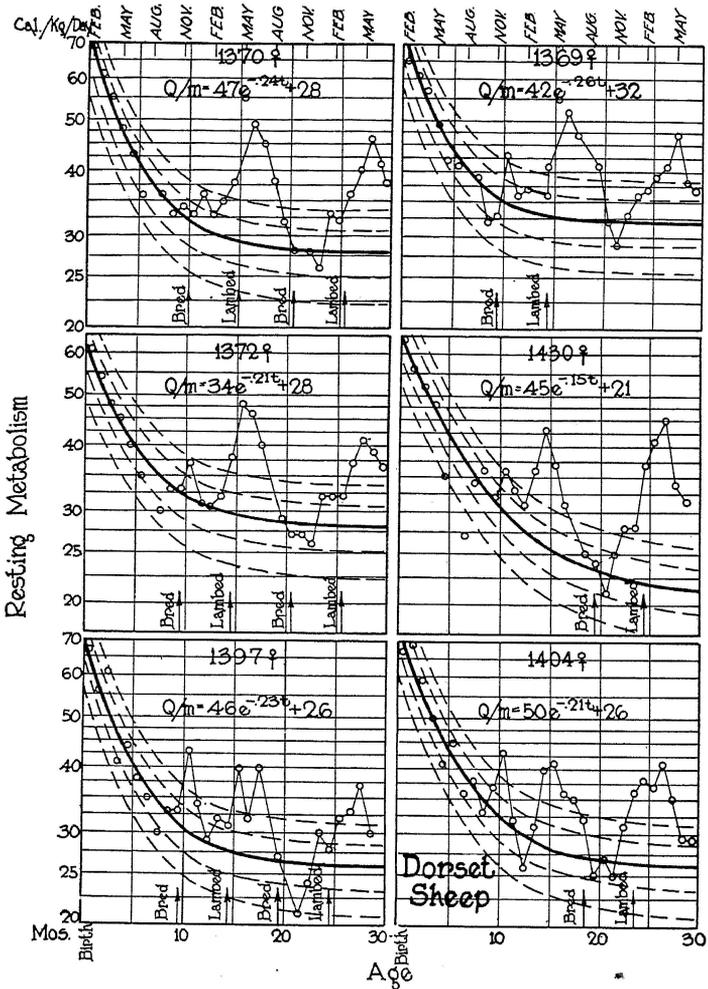


Fig. 3b.—Age curves of *resting* metabolism of individual sheep. Note the maxima of the cycles tend to come in May following shearing, and the principal minimum in November. See also the inset in Fig. 3c.

to say anything very definite at this time, concerning the relative contributions of each of these factors to the cyclic variations in metabolism. Since the wethers and females that were not bred, likewise show the cyclic variations, it is evident that there are other factors in addition to sex influencing the apparent seasonal variations in metabolism.

This problem is under active investigation. However, it may be permissible to call attention at this time to a gross arithmetical error in all the computations using body size as unit of reference. It is this:

The weight of the wool constitutes, before shearing, an important fraction of the total weight of the animal. In the preceding and in the present report, as also in the reports by Benedict and Ritzman, no adjustments were made for the wool weight. Therefore, before shearing, the apparent metabolism per unit weight (or area) is lower than it should be. Following shearing, there is an apparent (due to shearing) drop in the weight of the animals, with a consequent *apparent* increase in metabolism per unit weight.

The relatively simple and obvious problem of adjusting for the wool weight in sheep is a phase of the more general problem of adjusting the live weight of the animal to its "active mass." We have for example, a similar but more complicated problem in adjusting for the relatively inert fat deposits in the bodies of individuals of different degrees of fatness and different heights. This is merely another way of saying that the live weight of an animal is not a measure of its "active mass", and the custom of relating metabolism to surface area is an attempt to minimize these fluctuations in "active mass" by relating metabolism to a fractional power of live weight, instead of to weight itself; and the "surface law" may only be an attractive "explanation," or rationalization, of this difficulty.

We have already mentioned Benedict and Ritzman's contributions in this field. Lefevre and Auguet have built an elaborate calorimeter with refrigeration equipment for sheep, and they are at present making a thoroughgoing investigation of the influence of temperature on the metabolism of this species. André Mayer and associates also, are investigating similar problems as they relate to the rabbit. It would not be appropriate to discuss the remarkable results of the Paris investigations as they do not bear directly on the problem under immediate investigation, but we wish to call attention to their work, and to refer to some of their recent reports on this problem.

b. Basal Metabolism and Heat Increment of Feeding.—The lower left quadrant in Fig. 3c represents individual measurements of sheep in post-absorptive condition. The distribution of the data points are somewhat erratic, but an average equation was fitted to them as represented by the heavy continuous curves. The broken curve represents the resting metabolism of the population as in Fig. 3a. The difference between the resting and basal metabolism levels is seen to be of the order of 20%. The basal metabolism of the (single) wether is seen to be considerably below that of the females, mainly because the wether is much larger, and also much fatter, than the females.

c. Individual Differences in Resting Metabolism.—The curves of the individual animals shown in separate charts in Fig. 3a and 3b are brought together in the lower right chart of Fig. 3c. Individual differences

in sheep are as great as those in cattle—partly on account of differences in live weight of the animals.

d. *A Comparison of Our Curves With Published Data.*—The only published systematic measurements on the metabolism of sheep at dif-

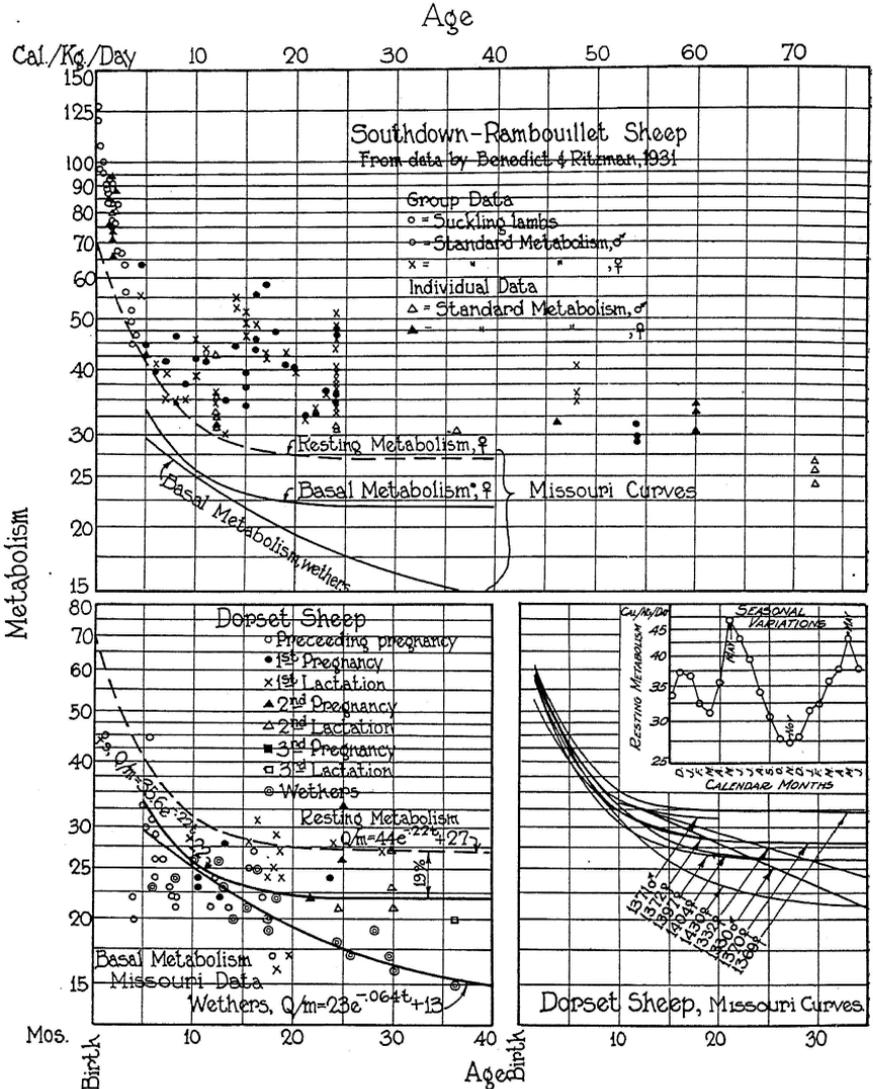


Fig. 3c.—Metabolism of sheep. The symbols in the lower left quadrant represent individual basal metabolism measurements. The heavy smooth curves represent the averages for seven females and a castrated male (wether). The broken curve represents the average resting metabolism curve of the female sheep population in Fig. 3a. The irregularity of the distribution of the data points is due to seasonal variations, shearing, pregnancy, and lactation. The lower right quadrant shows comparisons of age curves of metabolism of individual animals. The inset indicates seasonal variations when the averaging of the metabolism was done by calendar months instead of by age. The upper half of the chart gives a comparison of the data on standard metabolism as published by Benedict and Ritzman with our average resting and basal metabolism curves.

ferent ages are those by Benedict and Ritzman. We have plotted their data in the upper half of Fig. 3c. The *resting* and *basal* curves of our animals are there shown, for purposes of comparison, along with Benedict and Ritzman's measurements.

The difference between the values of Benedict and Ritzman and of our data may be due in part to the differences in live weight of the animals. This is shown in Fig. 4a, p. 55, of Missouri Research Bulletin 166, in which the curves based on Benedict and Ritzman's data are compared to ours, with metabolism per unit weight plotted against body *weight* (instead of age as is done in the present Fig. 3c). There, it is seen that the curves representing Benedict and Ritzman's data, especially for wethers, are *below* our *resting* metabolism curves. However, our *basal* metabolism values are always below Benedict and Ritzman's whether expressed as functions of age or of weight.

It was there pointed out that Benedict and Ritzman's animals were measured in the standing position while our animals, thoroughly trained and habituated to these measurements from the day of birth, were measured individually in the natural lying position. These factors (position and training) would tend to reduce our values considerably, at least 15 per cent. Also, our suckling lambs were separated from their mothers for 12 hours before measuring them for *resting* metabolism, while apparently this was not done in the case of Benedict and Ritzman's lambs. This would reduce our metabolism values during the suckling period. Furthermore, our *basal* metabolism values represent animals that fasted at least 48 hours, while Benedict and Ritzman's *standard* metabolism represents animals fasting only 24 hours.

Of course, as previously noted, there is a possibility that sheep exhale some methane, which on accumulation in the oxygen spirometer during the measurement might give an apparently lower oxygen consumption. We admit the existence of such a possibility for sheep as we did for cattle, but we do not believe that this would be sufficient to introduce an appreciable error.

3. Horses

a. Peculiarity of the Horse Data.—The horses, unlike the other classes of our animals, were measured in the standing position. The reason for this exception, as explained on page 57 of the preceding report, is that horses naturally stand up most of the time, even while sleeping; and this species, unlike the others, seems to be more at ease in the standing position than if *compelled* to lie down. Young colts are much more restless than any of the other species, so that our metabolism of the young animals includes the heat increment of the consequent fidgeting. But after they had worked in the field (on a regular farm

schedule) for several weeks, they seemed to have lost completely their restlessness, and remained quietly drowsing while being measured. This would tend to give an apparently lower metabolism at the later ages. However, the animals lost weight while working, thus increasing the metabolism per unit weight with the net result that the age curve was not greatly affected by the work at the more advanced ages.

b. The Age Curves of Resting and Basal Metabolism.—All our curves for horses are shown in Fig. 4. The upper 6 charts in Fig. 4 represent the curve of the individual animals, the lower left (No. 1) represents the curve of the population of the six animals; the chart in the center (No. 2) presents a comparison of the individual animals; the chart on the right (No. 3) represents individual "basal" measurements, 5-month averages (double circles), and the fitted curves for the basal and resting metabolism of the population.

The horse population is seen to be made up of females and geldings, some of which were "full-fed" and others "limited-fed". The full-fed animals tend to have a higher resting metabolism than the limited-fed, and the geldings tend to have a lower metabolism than the females.

We are not familiar with published data on the metabolism of growing horses, and so, of course, we can not say how our values might compare with those that might be obtained by others. We are confident that our data on horse metabolism, especially for the later ages, are thoroughly reliable.

4. Swine

a. Peculiarities of the Swine Data.—The animals at our disposal were obtained in connection with another investigation relating to factors influencing fertility in swine. In that connection, they were kept in rather confined quarters with no access to pasture. The animals were very poor breeders, and tended to get very fat. Indeed, at the later ages the animals were altogether too fat to be typical representatives of their kind in Missouri.

While being measured under proper conditions, the animals are absolutely quiet, more so than any other species investigated. On the other hand, when the animals are not in a mood for it, they give surprisingly erratic values for metabolism.

b. The Age Curves.—The data and curves of the individual animals are presented in Figs. 5a and 5b. The influence of lactation on metabolism are even more striking in swine than in cattle. This may be due in part to the fact that the animals lost weight very rapidly during lactation, with a correspondingly rapid increase in metabolism per unit weight.

The two charts in the center of Fig. 5b represent individual measurements of basal metabolism, together with the fitted curve to the basal

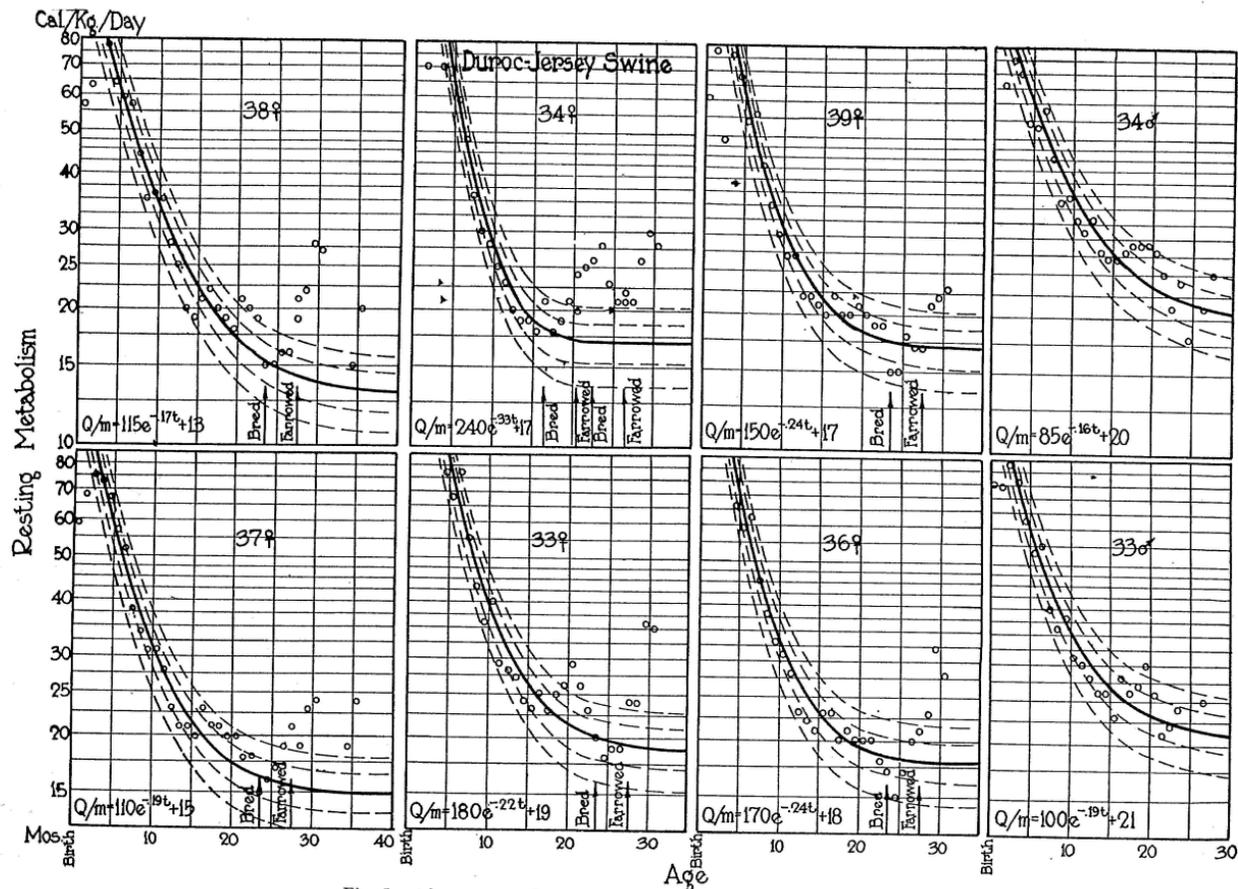


Fig. 5a.—Age curves of resting metabolism of individual swine.

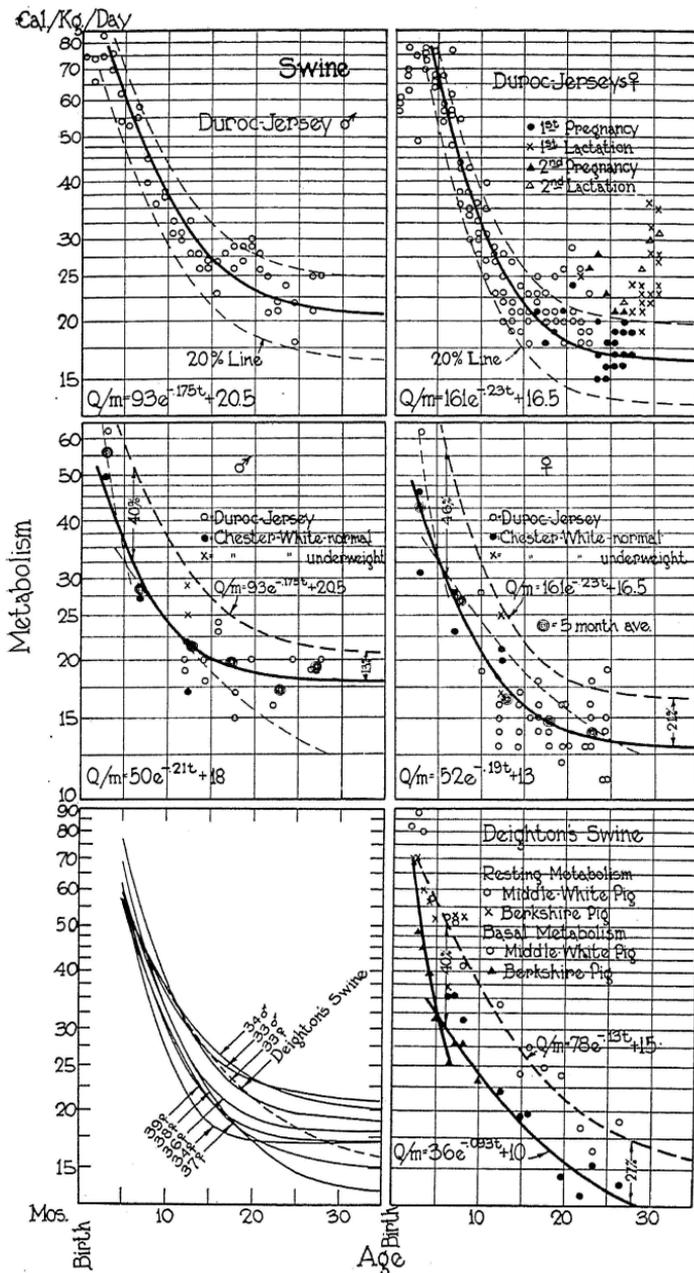


Fig. 5b.—Upper left chart represents the resting metabolism of a male hog; upper right chart represents the resting metabolism of our entire female population; the data points in the two center charts represent individual basal metabolism measurements, with the heavy smooth curve representing the fitted curve to the equation, and with the heavy broken curve representing the resting metabolism of the swine populations, and with the light broken curve representing the basal metabolism of Deighton's castrated males; the lower right chart represents the "resting" and the basal metabolism of Deighton's castrated males; the lower left chart represents a comparison of the individual fitted curves of the resting metabolism data.

data (solid curve) and also to the resting metabolism data (broken curve) of the swine population. The resting data for the entire swine population are shown in the upper right chart.

The lower left chart presents a comparison of individual curves of each of the animals under observation. The "resting" curve of Deighton's hogs is also drawn there (broken curve) for purposes of comparison.

The "resting" and basal metabolism data (and their fitted curves) of Deighton's hogs are shown in the lower right chart. Measurements taken 10 to 12 hours after feeding are taken to represent "resting" metabolism, while measurements made 48 to 72 hours after feeding are taken to represent basal metabolism. Deighton's animals were measured in a water calorimeter while they were in deep sleep. The very light, irregularly broken, lines in the two center charts represent Deighton's data for basal metabolism.

When the metabolism per unit weight values are plotted against *age*, then our animals appear to have lower metabolism than Deighton's; but when metabolism per unit weight is plotted against body *weight*, then our animals appear to have a higher metabolism than Deighton's animals. This is, of course, due to the fact that our animals are heavier at the given ages.

III. DOMESTIC FOWL

Our data on the domestic fowl are shown in the lower half of Fig. 6. The upper chart represents data by Mitchell, Card and Haines. As these two sets of data were discussed critically in pages 67 to 70 of Missouri Research Bulletin 166, there is nothing that we can add in this place that would shed further light on this problem. The numerical values for the metabolism of these two sets of data are presented at the end of this bulletin. It may be noted that, according to a report now in press, there is satisfactory agreement between metabolic values obtained on the same birds by the volumetric method here used, and Haldane's gravimetric method.

IV. THE WHITE RAT

The animals under consideration in this section are the same as those discussed in pages 71 to 76 of Missouri Research Bulletin 166, but about 6 months older; and the metabolism data are here presented as functions of age instead of weight.

The data are presented graphically in Figs. 7a and 7b. Curves 1 and 3 in Fig. 7a are age curves of metabolism per unit weight of individual rats growing more or less normally, while curves 2 and 4 represent similar curves for healthy but quantitatively undernourished animals. The age curves for weight (the light rising curves) are also given for purposes of

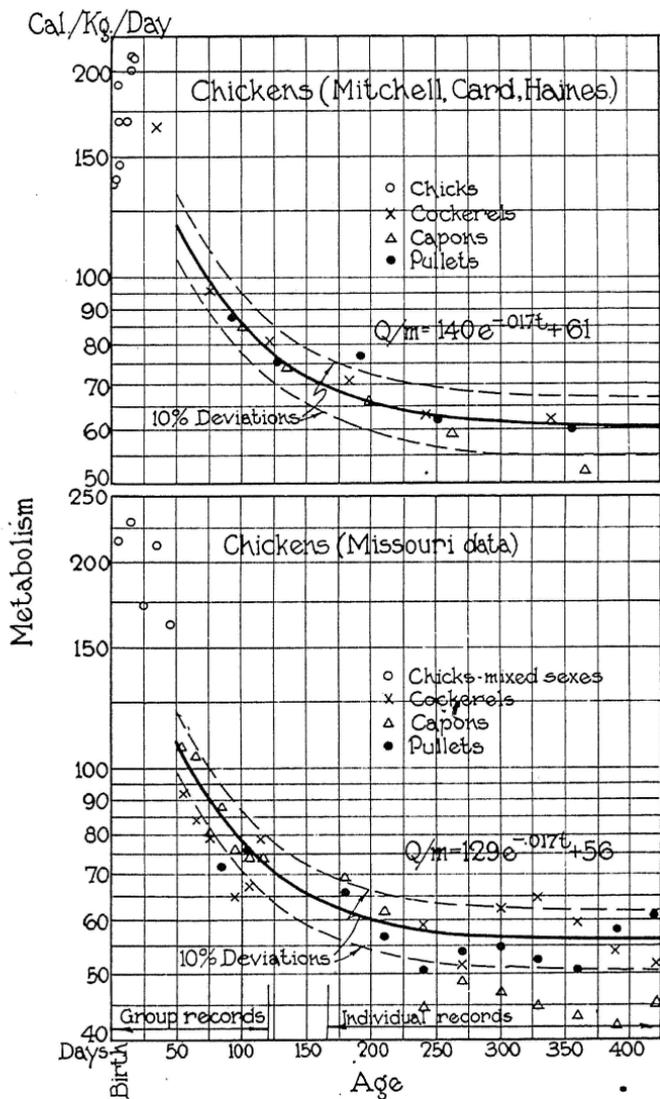


Fig. 6.—Age curves of energy metabolism of the domestic fowl. Lower chart our data; upper chart, data by Mitchell, Card, Haines.

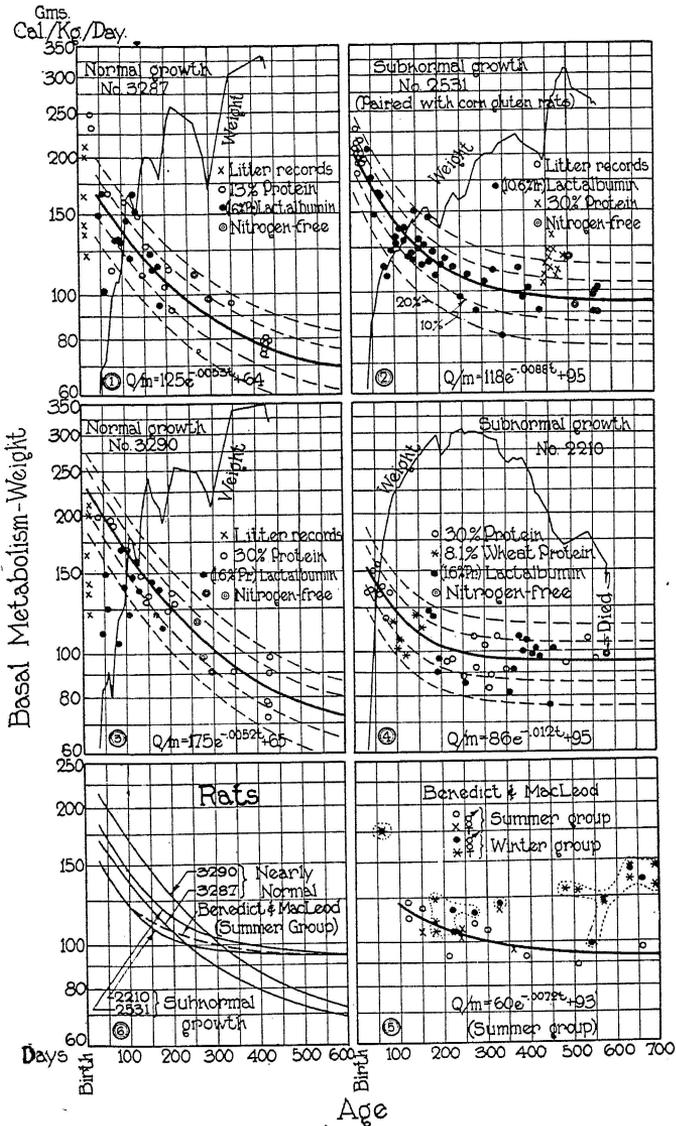


Fig. 7a.—Age curves of metabolism of rats. Curves 1 to 4 represent values of some of our individual rats grown on different diets. Curve 2 represents a rat receiving mostly an adequate diet qualitatively, but restricted to the same calorific intake as that consumed by the corn-gluten rats. The diets of the other groups are indicated on the charts. The weight curves (right lines) are given to indicate the influence of the nature of the diet on growth in weight, and as a semi-quantitative indication of the influence of body weight on metabolism. Curve 5 represents Benedict and MacLeod's summer group of rats, while the curves in 6 represent a comparison of curves 1 to 5.

indicating the extent of underweight in the chronically undernourished animals.

The four individual curves are compared in the lower left chart (No. 6). It is clear that at given ages the underweight rats have a much higher metabolism per unit weight than the normal rats. This is probably due to the fact, as previously explained, that the viscera (i. e., the "working" organs under basal conditions) constitute a greater proportion in the underfed than in the normal animal.

The lower right chart (No. 5) represents data by Benedict and MacLeod. We have fitted our usual equation to their summer group of data, including males and females. To avoid confusion, the winter groups are shown in broken enclosures. This summer group average is also shown in chart 6 for purposes of comparison. It is seen to agree with our subnormal individual curves, but rather high as compared to our normally-growing animals.

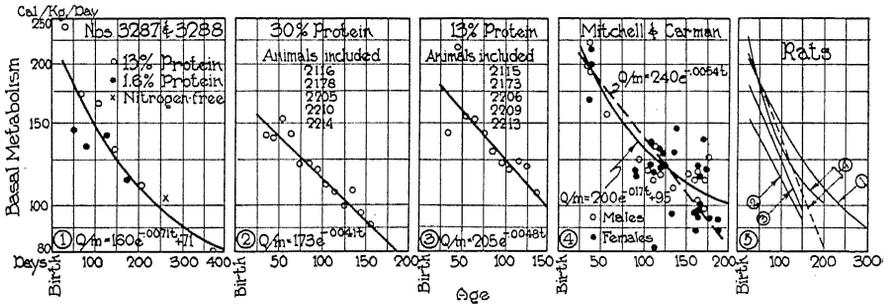


Fig. 7b.—Age curves of metabolism of rats, continued. The number of animals included in each group and the protein planes fed are indicated on the chart. Curves 1, 2, and 3 represent original data; curve 4 represents data by Mitchell and Carman; while 5, the chart on the extreme right, represents comparisons of curves 1 to 4.

Curves 1, 2, and 3 in Fig. 7b represent three groups of animals on different diets, for the younger ages. As previously indicated, if attention is confined to only a part of the segment of the age curve, then the simple exponential equation (not including the constant C) fits the data satisfactorily. The advantage of using the simple exponential equation 2a, is that k represents, without qualifications, the relative (or when multiplied by 100, the percentage) decline in metabolism per unit time. In the case of the curves in 7b, the value of k (for curves 2, 3, and 4) is of the order of -0.004 to -0.005 , which means that the metabolism per unit weight declines at the rate of 0.4 to 0.5 per cent per day (or 12 to 15 per cent per month). This may be compared directly with the decline in metabolism in other species. Thus, for example, the decline of Q/m with age for the earlier ages in cattle (see Fig. 2a) is of the order of 4 to 5 per cent per month, as compared to 12 to 15 in rats (Fig. 7b). That is to say, assuming that the cattle and rat curve

segments to which the equation was fitted represent equivalent periods of development in the two species, then the decline in metabolism with increasing age in rats is 3 times as great as in cattle. The differences in *percentage decline* in metabolism of cattle and rats are probably related not to the *absolute* weights of the animals in these two species, but rather to the relative declines in growth rates.

The curve 4 in Fig. 7b represents data by Mitchell and Carman. The male and female data are combined in the fitted equations.

The curves in 5, Fig. 7b, represent a comparison between curves 1, 2, 3 and 4. It is seen that curve 4 (Mitchell's data) is a bit high, but, in general, agrees quite well with our data. As Mitchell used an entirely different method for measuring the metabolism of his rats, this agreement speaks well for the very simple method for measuring metabolism as employed by us (described in pages 71 to 76, Research Bulletin 166).

We next come to the consideration of the exceedingly important problem of the relative influences of age and body weight on metabolism during growth. This might be conceivably determined by letting the animal increase in age while holding it at constant body weight.

We attempted to do this in a tentative and halting fashion on a few rats by confining the protein in their diets to corn gluten, but permitting the animals to take freely of this inadequate diet. The animals did make some gain in weight on this diet; but the rate of growth is very slight as compared to animals on a complete diet.

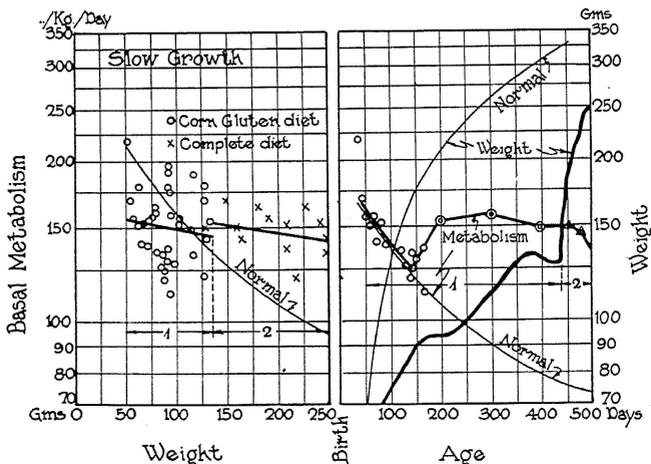


Fig. 7c.—A comparison of growth and metabolism of normally growing rats with stunted rats on a corn gluten diet as sole source of protein. On the right side, the heavy curves represent the stunted animals while the light lines represent a normal animal. On the left side, circles and heavy curve represent the stunted rats on the inadequate (corn gluten) diet while the x's and heavy curve represented the stunted rats after they were placed on an adequate diet. The light curve, as before, represents a normal animal. Periods 1 and 2 shown on the chart represent respectively the periods on the inadequate corn gluten and on an adequate diets.

The results are presented in Fig. 7c. The right half represents the age curves of growth in weight of a stunted animal (heavy rising curve) up to about 430 days and of a normal animal (light rising curve); also of metabolism per unit weight of a stunted animal (heavy curve) and of a normal animal (light declining curve).

The stunted animal gained about 35 grams during the age interval of 4 to 15 months (period 1), while the normal animal gained about 150 grams. The metabolism per unit weight in the stunted animal remained nearly constant from 200 days on, while in the normal it declined from about 115 to about 75 Calories per kilo per day. This appears to indicate that body weight is by far the most influential factor in limiting the metabolic rate, and that age is a relatively negligible factor during this age interval. Age, or time, is not, of course, a part of the animal system; therefore when we speak of time as affecting the organism, we merely use a convenient figure of speech which can be expressed quantitatively. The quantitative aspect of this figure of speech is statistically valid under certain conditions of growth, and not valid under others of which the present is an example (see Fig. 20, p. 62, and the discussion relating thereto in Missouri Research Bulletin 97). The stunted rat under consideration, while old in days, is apparently young in physiological development and its metabolism per unit weight is accordingly high. The relative absence of adipose tissues in the stunted rat may be a factor contributing to the high metabolism.

When, at age 440 days, the animal was placed on an adequate diet (period 2), it promptly began to gain in weight, and the metabolism per unit weight began to decline; but the decline in metabolism was not as rapid as was expected. (This may be due to secondary specific dynamic action.)

On the left side of Fig. 7c, the same metabolism data are plotted against body weight. Circles (period 1) represent the period of inadequate diet; X^s (period 2) represent the period on adequate diet. The heavy lines represent the average curves (fitted by the method of least squares). The light lines represent the curve of a normal growing rat. The slope of the metabolism curve of the experimental rat is very slight as compared to that of the normal rat; age is an insignificant factor. We expected a very steep slope for the period of adequate feeding (period 2, Fig. 7c). This expectation was not realized. This experiment needs to be confirmed before advancing explanations for this phenomenon.

V. ANALYSIS OF AGE CHANGES OF BASAL METABOLISM PER UNIT WEIGHT OF PUBLISHED DATA ON HUMANS AND PIGEONS WITH SPECIAL REFERENCE TO SENESCENCE.

1. Humans

The importance of the human data for the formulation of a broad generalization on metabolism has been discussed on pages 77 to 82 of Missouri Research Bulletin 166.

As before, we shall use the extraordinary complete series of data on humans by Benedict and his associates; and, by way of check, also insert a series of values on adults by Boothby and Sandiford.

a. Age Curve During Active Growth.—The data are shown graphically in Fig. 8a. The upper chart represents females, the lower chart males. All the data by Benedict and associates, from birth to 88 years, are included. Equation (2b) was fitted by the method previously described and lines representing 10% and 20% deviations are also given.

The observed values for Q/m when plotted against age are seen, in Fig. 2a, to be scattered over a wider zone than when plotted against weight (pp. 79 and 80, Research Bulletin 166). That is to say, the metabolism per unit weight is more closely correlated with body weight than with age. This is especially true as regards the data for females and particularly those following age of 30 years. These fluctuations must be due to the variability of the population as regards their weights and build at given ages.

b. Age Curve During Adulthood (Period of Senescence).—There are four notable discussions in the periodic literature regarding the age course in metabolism during adult life (following age 20 years), namely, those by Zuntz and Loewy, by Harris and Benedict, by Lusk and Du Bois, and by Benedict.

Zuntz and Loewy appear to doubt that there is an appreciable decline in metabolism (per unit area): "Diese zeit umfast die spanne vom 26 bis zum 52 Lebensjahr. Innerhalb dieser Zeit war keine vom Alter ohhängige Änderung des Umsatzes nachweisbar." Lusk and Du Bois likewise seem to doubt such a decline, while Harris and Benedict, and Benedict seem to be inclined to the view that, other conditions being the same, there is a decided decline in metabolism even at constant body weight with increasing age. It should be noted, however, that Lusk and Du Bois, in their textbooks on nutrition and metabolism (Lusk 1928, p. 139; Du Bois, 1927, p. 200) present metabolism standards indicating declines in metabolism with increasing age during adult life.

As these data are of considerable interest to us in indicating what possibilities we may expect to find in our still immature farm animals

under observation, it may be appropriate to examine the quantitative properties of these published data in some detail.

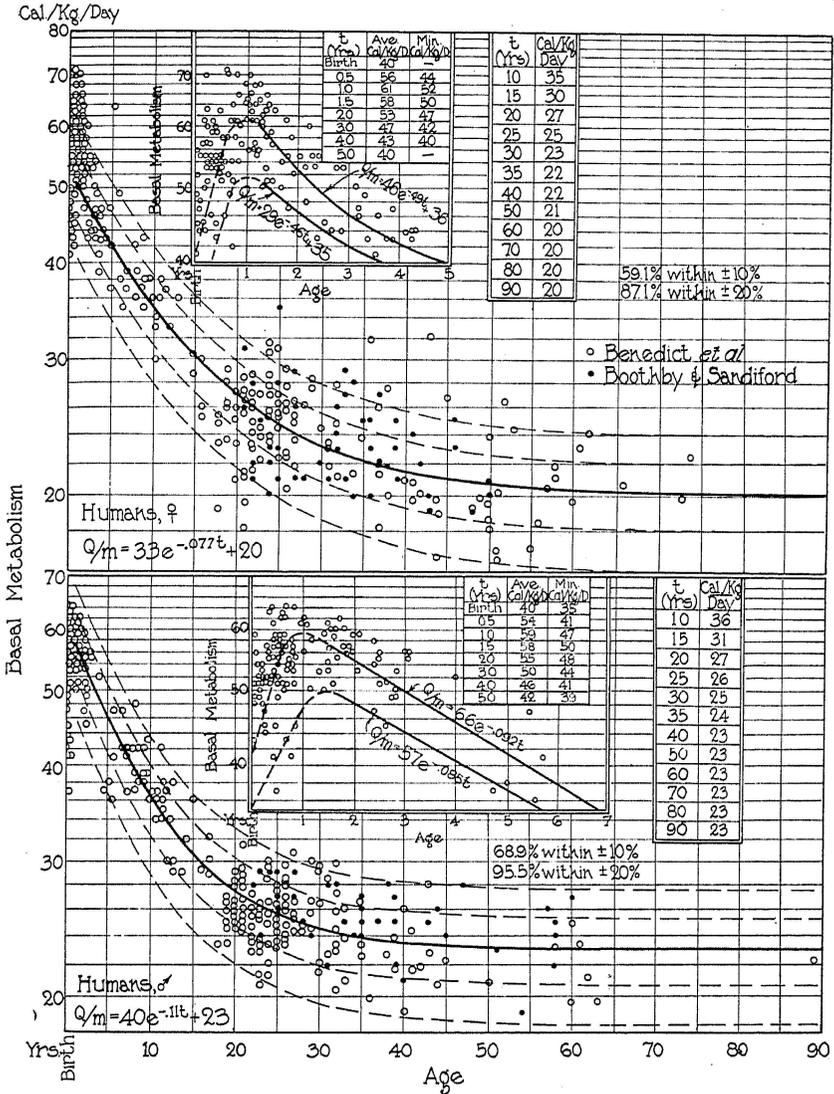


Fig. 8a.—Basal Metabolism per unit weight in humans as functions of age. Open circles represent data by Benedict and associates; solid circles represent data by Boothby and Sandiford. The insets represent on a magnified scale the segments of the curve between birth and five years. The upper curve in the insets represent the averages of the data, while the lower curves in the insets represent the minima of the data.

For this purpose we have plotted the data, in Fig. 2b, on arithlog paper and fitted to them linear ($Q/m = A + Bt$) and exponential ($Q/m = Ae^{\pm kt}$) equations. In these equations B represents the absolute loss in metabolism (Calories) per unit weight per year, and k represents the relative (or when multiplied by 100, the percentage) yearly decrease, or increase, in metabolism with increasing age. Both types of equations were fitted to the data by the method of least squares; so that, within the limits of applicability of this method, guessing is thereby eliminated from the fitting of the equations to the data.

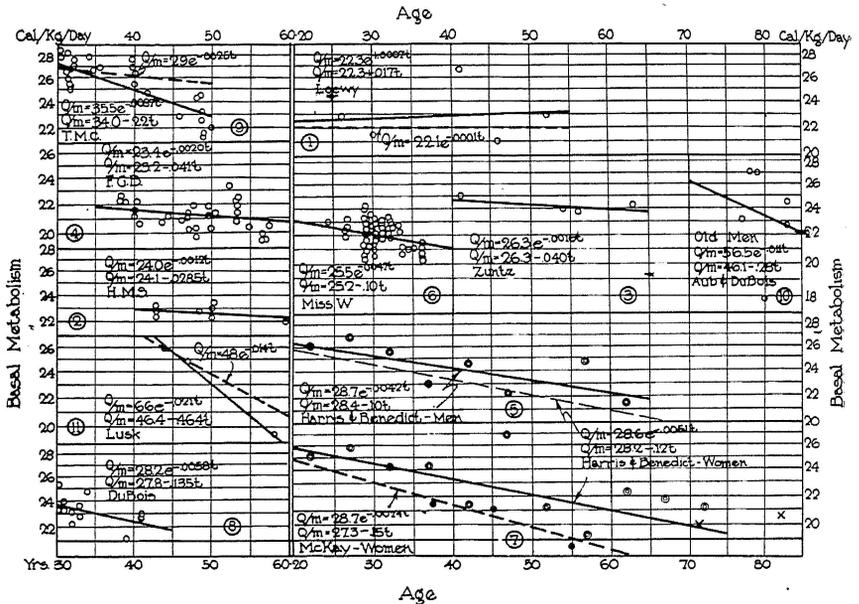


Fig. 8b.—The decline of metabolism per unit weight with increasing age in adult humans. Double circles represent population averages. The single circles represent individual measurements, and with the exception of curve 10, represent the same individuals. The exponents in the exponential equation represent the relative, or when multiplied by 100 the percentage, decline per year. The coefficients of the linear equations represent the absolute decline in Calories per kilogram per year. The curves are numbered in the order of their magnitude of the yearly declines (k) beginning with the lowest decline. The continuous curves represent a fit to all of the data points (broken curve (9) does not include values following 46 years; broken curve (2) does not include the observation at 58 years, and broken curve (1) does not include the value at 41 years). All equations were fitted by the method of least squares. The x's (in section 7) represent the average of data on elderly women (ages 66 to 86 years) published by Benedict & Meyer, and inserted after this chart was prepared, and so are not included in the fitted equation for women. The data point (x) at 71.3 years represents Benedict's subjects 1 to 12, covering ages 66 to 76 years. The data point (x) at 82 years, represents Benedict's subjects 13 to 23, covering ages 77 to 86 years.

In Fig. 8b, each set of data is designated by a number, the curves being numbered in order of their decline, k, in metabolism with increasing age. Curve (1) representing the age changes in metabolism of Loewy, shows the least decline with age. The continuous curve includes all measurements on Loewy and shows that the metabolism *increases* with

increasing age at the rate of 0.07 per cent per year, or at the rate of 0.017 Calories per kilo per year. If the observation at 41 years is omitted, then we get the broken curve which is practically horizontal; that is, there is no decline in metabolism for the given age interval of 26 and 53 years. Curve (2) on H. M. S. (data by Benedict) shows a decline of 0.13 per cent per year, or 0.028 Calories per kilo per year between age limits of 42 and 59 years. Next come the data on Zuntz, and so on as shown in Table 1. The broken curve for T. M. C. does not include the data following 41 years, while the continuous curve includes all measurements. The broken curve for Lusk does not include the last measurement, while the continuous curve includes all three measurements. The double circles for curves (5) and (7) represent averages of a number of individuals, while the single circles represent individual measurements of individuals.

TABLE 1.—CHANGE IN BASAL METABOLISM WITH INCREASING AGE IN HUMANS

Serial Number on the Chart	Subject	Authors	Age Range in Years	100k (yearly percentage decline in metabolism per kilo)	B (absolute decline in daily metabolism per kilo per year)
1	Loewy	Zuntz & Loewy	26-52	+0.07 & -0.01	+0.017
2	H. M. S.	Benedict	43-59	-0.02	-0.029
3	Zuntz	Zuntz & Loewy	41-63	-0.16	-0.040
4	F. G. B.	Benedict	39-58	-0.20	-0.041
5	Population of Men	Harris & Benedict	22-62	-0.42	-0.10*
6	Miss W	Benedict	25-36	-0.47	-0.10
7	Population of Women	Harris & Benedict	22-72	-0.51	-0.12*
8	Du Bois	Lusk & Du Bois	30-41	-0.58	-0.14
9	Population of Women	McKay	37-55	-0.74	-0.15
10	T. M. C.	Benedict	31-49 & 31-41	-0.87 & -0.25	-0.22
11	Population of old men	Aub & Du Bois	77-83	-1.1	-0.28
12	Lusk	Lusk & Du Bois	44-58 & 44-47	-2.18 & -1.4	-0.46

*Harris and Benedict (1919, p. 126) give the yearly decline as 0.112 Calories for men and 0.124 Calories for women, but they included the age period of 15-19 years which we did not, as we wished to confine our computations for the period following *active* growth.

Fig. 8b and Table 1 indicate that individuals vary considerably as regards their decline in metabolism with increasing age. Subjects 1, 2, 3, and 4 (Table 1) show very slight declines, while subjects 9 and 11 show considerable declines. The curve of subject 9 (T. M. C.) is unusual in the fact that the decline is very slight for the age interval 31-41 year—less than half of the decline for subject 8 for the same interval; and then, following 46 years, there was a sudden decline which brings down the average decline for the interval of 31-49 years to 0.87 per

cent per year. The most rapid decline is shown by subject 11, unusually rapid in comparison with the other curves. Lusk and Du Bois explain the decline of this subject by his strenuous life in the earlier years, with an accompanying relatively high metabolism, and by the "cage life" of later years with accompanying low metabolism. These two circumstances tend to give a resultant exaggerated rapid decline. This explanation appears reasonable, and it may apply to the drop in metabolism of subject 9 (T. M. C.) following age 46 years. The writer understands that Subject 9 has reduced considerably his program of physical activity following age 46 years when he suffered an attack of typhoid fever.

These individual variations indicate that generalizations are not permissible on the basis of data on one or two individuals and emphasize the importance of statistical studies on populations if one is to arrive at reasonable figures. The data by Harris and Benedict (represented in Fig. 1b by double circles, and numbered (5) and (7)) represent such statistical values. The decline in metabolism with increasing age of these populations are seen in Fig. 8b, and Table 1, to be about midway in the series of individual curves. In other words, while there are very considerable individual differences in regards to the decline in metabolism with increasing age (due to age as such and also influenced considerably by the vigor and physical activity of the individual), it is safe to say that, on the average, the metabolism per unit weight tends to decline with increasing age (for the given age intervals) at the rate of about 0.5 per cent per year. While there is, of course, uncertainty concerning the relative contributions of the various causative agencies to these declines, there can be no doubt that the metabolism, on the average, does decline with increasing age.

c. Race and Sex Differences in the Age Curves.—Before concluding this section, it may be interesting to discuss briefly the age changes in metabolism of another race of the human family in comparison with the metabolism of white Americans. Mr. R. P. Combs of Kansas City, Missouri, a breeder of dairy cattle and saddle horses, has suggested that racial and individual differences in energy metabolism in farm animals might be made a basis for selection of promising animals. Since but few data, if any, are available for a comparison of racial characteristics of metabolism of farm animals, and since the experimental errors in metabolism measurements are very much greater for farm animals than for humans, therefore human data are likely to furnish the best indications of racial differences, if present. This explains in part the interest of agriculturists in this matter.

Benedict and associates are giving considerable attention to the problem of racial differences in human metabolism. One of these in-

vestigations was carried out at Benedict's request by Hicks, Matters, and Mitchell on Australian native aboriginals of the Kokata tribe at the Kooniba Mission in South Australia. We have plotted these metabolism data in Fig. 8c for males and fitted equations in the same manner as was done for the data in Fig. 8a. Fig. 8c and Table 2 lead to the following conclusions:

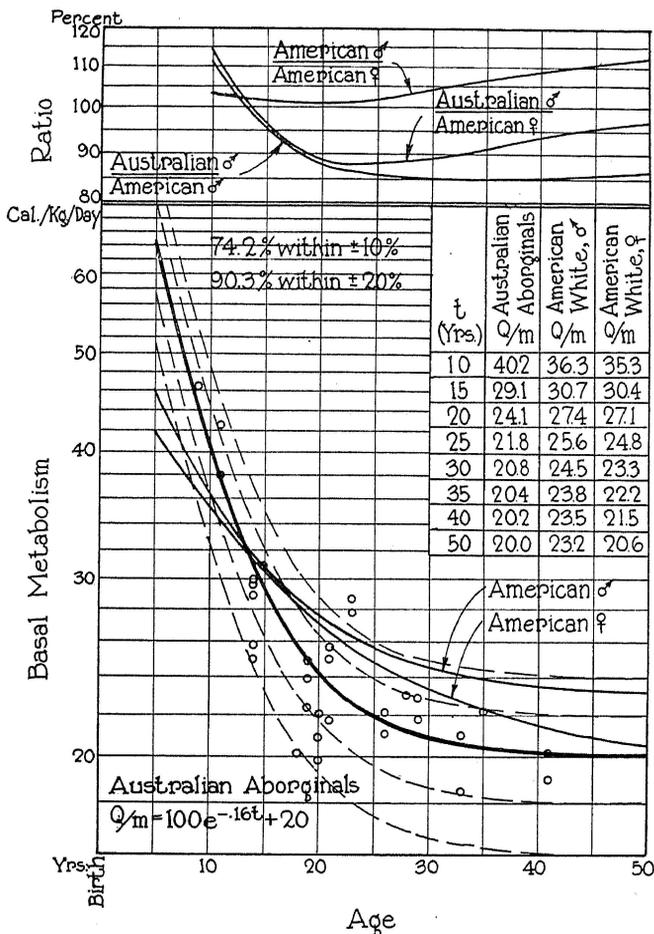


Fig. 8c.—The basal metabolism per unit weight as a function of age in Australian aboriginals, males. The circles represent observed values, the heavy curve represents the average given equation. The broken curves represent 10 and 20% deviations from the average. The lighter continuous lines represent the age curves of American white males and females copied from Fig. 8a. The upper portion of the chart represents ratios of basal metabolism of (1) American males to American females; (2) Australian males to American females; and (3) Australian males to American males (see Table 2). Note that all curves nearly meet at puberty; that preceding puberty the metabolism of Australian aboriginals is greater than of American whites, and that the reverse is true following puberty; the metabolism of American males is at all ages higher than of females, but they are nearest together at about 15 years.

TABLE 2.—THE INFLUENCE OF SEX AND RACE ON THE RELATIVE BASAL METABOLISM OF AMERICAN (WHITE) MALES AND FEMALES, AND AUSTRALIAN ABORIGINAL MALES

Age Years	Basal Metabolism, Calories per Kilo per Day					
	Australian Males	American Males	American Females	Percentage of		
				Austr. Male to Amer. Male	Austr. Male to Amer. Female	Amer. Male to Amer. Female
10	40.2	36.3	35.3	110.7	113.9	102.8
20	24.1	27.4	27.1	88.0	88.9	101.1
30	20.8	24.5	23.3	84.9	89.3	105.2
40	20.2	23.5	21.5	86.0	94.0	109.3
50	20.0	23.2	20.6	86.2	97.1	112.6

(1) There are undoubted differences in basal metabolism of American white males and Australian Aboriginal males. It is impossible to say at this time concerning the relative contributions of the two most probable causative factors of these differences, namely environment and heredity. The American Negro should be a suitable subject for such a study.

(2) The curves of American and Australian males cross at about 13 years (puberty). Preceding this age, the metabolism of Australians is higher—and the earlier the age, the higher in comparison is the metabolism per unit weight of Austrians over Americans. Following this age, the metabolism of American males is higher than of Australian males. At age 8 years, for example, the metabolism of the Australian male is almost 20% above that of the American white male; while at age 40 years, the metabolism of the white male is about 6.5% above that of the Australian male. Assuming that metabolism is an index of vigor, then the Australian aboriginal would be said as having a more vigorous childhood and youth and a less vigorous adulthood than the American white, which is, perhaps, in agreement with experience. It would be interesting to know whether under the same conditions the duration of life is greater in the white American than in the Australian aboriginal—that is, whether duration of life is a function of vigor or physical condition (assuming that basal metabolism is an index of vigor). It must be noted, however, that preceding puberty the Australian males are lighter, and following puberty, they are heavier than American white males (see Table 3): this may explain the differences in metabolism per unit weight in the two races of men.

(3) It is interesting to note that following 13 years, the age curve of the American females approaches more closely the age curve of the Australian male than of the American male. This is simply because the metabolism of the American female is below that of the American male. All three curves (American male and female and Australian male)

practically meet at puberty (13-15 years). These phenomena as they relate to body weight were discussed on pages 78 to 82, Missouri Research Bulletin 166.

TABLE 3.—THE COURSE OF BODY WEIGHT AND BASAL METABOLISM IN HUMANS WITH INCREASING AGE

Age Years	Body Weight, Kilograms			Basal Metabolism Per Day					
	American		Austr. Aborig.	Per Kilogram			Per Individual		
	Males	Females		American		Austr. Aborig.	American		Austr. Aborig.
			Males	Females	Males		Females		
5	19.0	17.2	----	42.0	40.0	64.0	798	688	----
10	27.0	27.0	26.0	36.3	35.3	40.2	980	953	1045
15	48.0	44.0	44.5	30.7	30.4	29.1	1474	1338	1295
20	63.8	54.3	58.5	27.4	27.1	24.1	1748	1472	1410
25	63.0	54.2	69.5	25.6	24.8	21.8	1613	1344	1515
30	62.5	55.0	73.0	24.5	23.3	20.8	1531	1282	1518
35	66.2	55.5	73.5	23.8	22.2	20.4	1576	1232	1499
40	64.0	58.7	74.0	23.5	21.5	20.2	1504	1262	1495
50	64.4	64.6	----	23.2	20.6	20.0	1494	1331	----

2. Pigeons and Doves

Data on pigeons and doves are plotted in Fig. 9. As the pigeon reaches practically mature weight at about three months of age, therefore charts 1 and 2 in Fig. 9 represent metabolism during adulthood, that is during the period of senescence, corresponding to the period in man following age of about 20 years.

From chart 1, Figure 9, it is seen that the basal metabolism per kilo per day in the female dove declines from 122 Calories at 5 months to 104 Calories at 60 months, or as indicated on the chart, the decline is 0.3 per cent per month, or 3.6% per year. We have seen (Fig. 8b) that in human females the decline is about 0.5 per cent per year, which is about $1/7$ of the rate of decline in doves. The decline in the male doves is 0.5 per cent per month, or 6.0 per cent per year. In human males, the average decline appears to be of the order of 0.4 per cent per year, or $1/15$ as rapid as in the dove. Of course, these comparisons must be considered as first, and very crude, approximations to the truth. We, nevertheless, have here a beginning towards a comparative physiology of metabolism during the declining phase of the life cycle.

A curious fact in this connection is that the metabolism in the female dove or pigeon is higher than in the male, and the decline in metabolism with age is greater in the male than in the female. This is just the opposite of what we found for humans (Fig. 8b). The curves for data sets 1 and 2, Fig. 9, were fitted by the method of least squares, so these differences are not due to errors in drawing the curves.

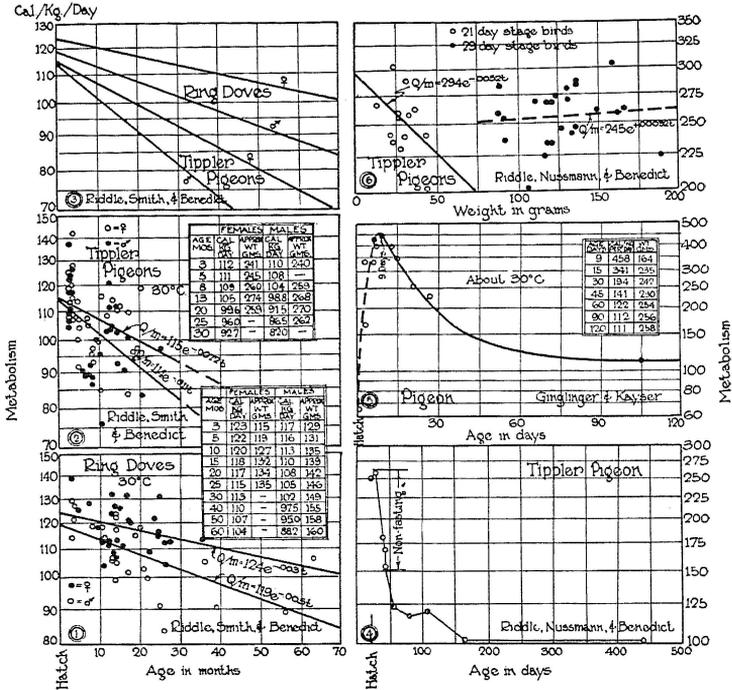


Fig. 9.—Metabolism of pigeons and doves. Sources of data are indicated on the chart. The curves in (1), (2), and (6) were fitted to the data by the method of least squares. The data in (4) and (6) were published by Riddle, Nussmann, and Benedict in terms of Calories per square meter per day; we converted the data, for the present chart, into Calories per kilo per day. We chose only such of the Ginglinger and Kayser data as were obtained at an environmental temperature of about 30°C. We consider the curves in (1) and (2) as age curves during senescence (as in Fig. 8b for humans) rather than age curves of growth. (3) merely represents a compact comparison of the fitted curves in (1) and (2).

However, according to Riddle, who kindly furnished the unpublished numerical data for charts 1 and 2, Fig. 9, these birds were measured at 30°C, and there is a “differential response of male and female ring doves to metabolism measurements at higher and lower temperatures”; and “that the metabolism of the male suffers a greater decrease with increase of external temperature than does that of the female” (Riddle, Christman, and Benedict). Under date of July 16, 1932, Riddle wrote to the author: “That statement (that the metabolism in the female dove is higher than in the male) would be true only if you added, ‘when measured at 30°’, and there would be other qualifications—such as, the inclusion of females and near the *ovulation* stage of reproduction. Even with the latter inclusion the data of Riddle, Christman, and Benedict, *Am. J. Physiol.*, Vol. 95, p. 111, 1930, show the metabolism of ring

doves (common pigeon data, comparable and adequate; not yet published) both at 15° and 20° is higher in the male; it is lower at 30° in the male”.

The curves in chart 3, Fig. 9, present a comparison of the metabolism per unit weight of doves and pigeons.

The data in charts 1 and 2 are *basal* metabolism data obtained at an environmental temperature of 30° C.

While preparing charts 1, 2, and 3, Fig. 9, we received a reprint from Riddle on “Metabolism During Growth in a Common Pigeon”, by Riddle, Nussmann, and Benedict, and we thought that it would be interesting to plot these new data in the same manner as we have plotted charts 1 and 2, with the results shown in charts 4 and 6 of Fig. 9. In 4, the metabolism data are plotted against age. The metabolism during the first 150 days is seen to decline from about 250 to 101 Calories per kilo per day. It is somewhat difficult to interpret these results in view of the fact that the measurements preceding 50 days were made on birds which were not in post-absorptive condition while those following this age were made with the birds in post-absorptive condition.

The data in Chart 6 represent the metabolism of two groups of birds of constant ages: 21 day stage (3 days after hatching) and 29—day stage (11 days after hatching), but having different body weights. The curves represent equations fitted by the method of least squares. From the distribution of the data points, it appears that the average metabolism per unit weight of the 11-day birds is about the same as of the 3-day birds, and that the differences in slopes of the fitted curves to the 3 and 11-day birds are due to differences in the amount of food in the birds of different weights at the two stages.

Chart 5, Fig. 9, representing data by Ginglinger and Kayser gives an interesting age curve of metabolism for the earlier stages of growth, comparable in shape to the curves of humans (see Fig. 8a, and of farm animals, Figs. 10a and 10b). The metabolism values are, however, unusually high, especially in the very early stages, as compared to Riddle and Benedict’s values.

VI. ADDITIONAL NOTES ON THE EARLY POSTNATAL RISE AND DECLINE IN METABOLISM

This phenomenon has been discussed in detail in connection with the life curve of metabolism of the domestic fowl (page 6), and also in connection with the age curves of humans (Fig. 8a) and pigeons (Fig. 9). In this section, we merely wish to present our data on farm animals in the form of graphs.

These data (covering the period from birth to 5 months) are shown in Figs. 10a and 10b.

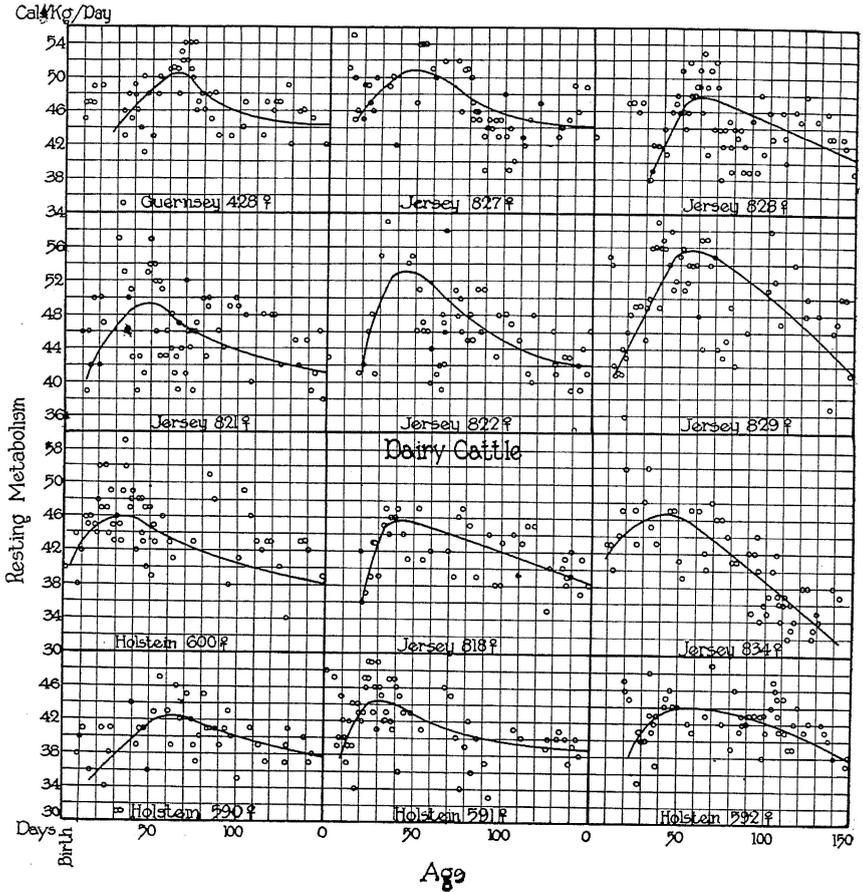


Fig. 10a.—Rise and decline in metabolism per unit weight plotted against age, for very young dairy calves.

Fig. 10a is given entirely to dairy calves. It shows, among the many regularities, that the metabolism rises from about 34 to 42 Calories

per kilo per day shortly after birth, to about 50 to 55 Calories at one to two months—when it is at a maximum.

The other species of farm animals, the curves of which are shown in Fig. 10b, naturally differ with respect to the initial level and the age of maximum metabolism. The maximum occurs later in swine, and much earlier in horses.

It is necessary to emphasize the difficulty of keeping a very young animal quiet and relaxed. This applies especially to horses. They were exceedingly nervous and apprehensive when separated from their mothers. In view of these difficulties, these curves will naturally have to be verified.

The possible causes of the shape of the metabolism curve have been discussed in the introduction (page 6).

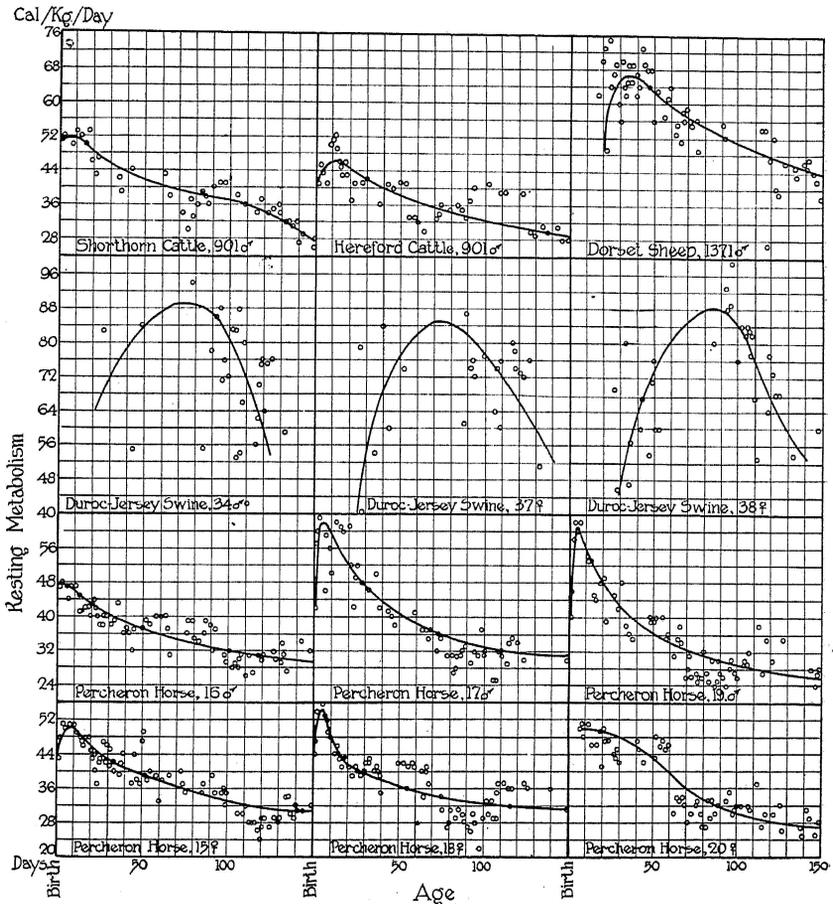


Fig. 10b.—Rise and decline in metabolism per unit weight plotted against age for very young, steers, sheep, swine, and horses.

VII. SPECIES COMPARISONS OF AGE CHANGES IN ENERGY METABOLISM PER UNIT WEIGHT WITH NUMERICAL SUMMARIES OF THE DATA.

Since the energy metabolism tends to be a function of weight raised to some fractional power, rather than to weight directly, therefore species comparisons in *age* changes of metabolism per unit weight do not have the same significance as comparisons of *weight* changes in metabolism per unit weight. Yet, such a comparison will not be without interest, and this section is therefore devoted to this problem—rather, to an introduction to this problem.

The comparisons are presented in graphic form in Fig. 11, and also in numerical form in Tables 4 to 15. Since body weight is an important factor affecting the metabolic rate, therefore the tables also include columns for the average live weights of the animals under consideration. Values for total metabolism per individual per day are also given:

Curves 1 and 2 of the pigeons represent the period of senescence rather than of growth, as this species matures at about age three months. This may be largely true as regards curve 3, representing Benedict and MacLeod's summer group of rats. But the other curves represent periods of active growth in weight.

As equal slopes on arithlog paper represent equal percentage declines in metabolism per unit weight, therefore the slopes of the curves represent proportional percentage declines in metabolism per unit weight with increasing age. By actually measuring the slopes of the curves in various regions, we find that the slope at 10 months for the curve of the rats is the same as the slopes for 6 months in the curves of chickens, 5½ years for humans, 8 months for sheep, 10 months for Jersey cattle, 7 months for Holstein cattle, 13-14 months for swine, 5½ months for horses. The slope of the curve for a 5-month rat is the same as the slope for 4-month chickens; 3-year humans; 4-month swine. How should one interpret the fact that the percentage decline in metabolism per unit weight is the same in a 10-month-old rat (which is quite mature at this age) as in a 10-month Jersey calf (which is very immature at this age)? Evidently the relative stages of physiological maturity do not explain the similarity in slopes at 10 months in the two species. It may, conceivably, be associated with the percentage decline in the growth rate. We hope to report on this and related problems in a future paper.

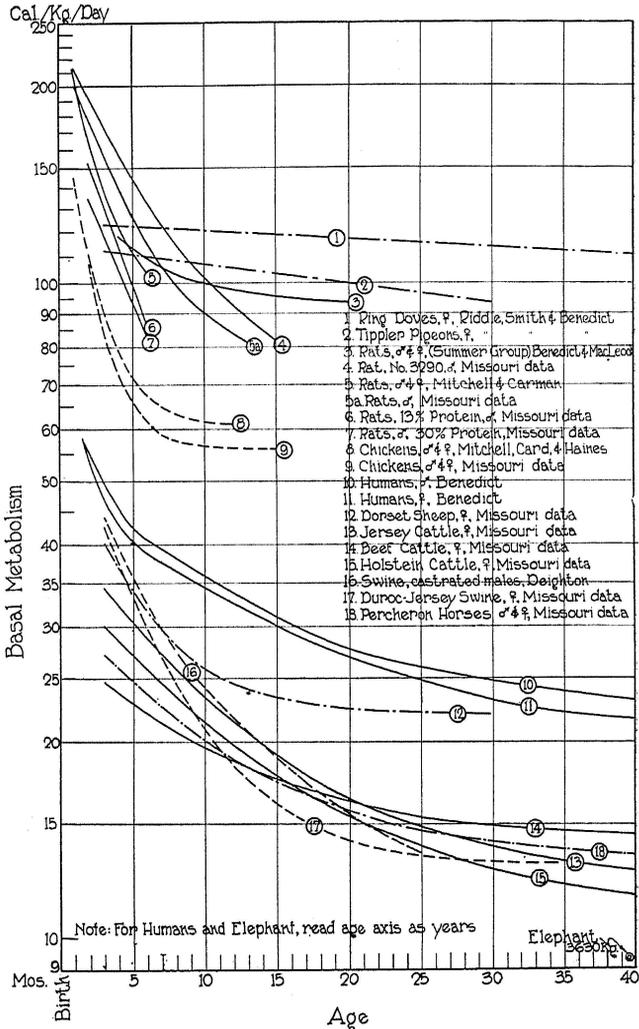


Fig. 11.—Species comparisons of age changes in metabolism per unit weight plotted on an arithlog grid. Ages are in months, except for humans and elephants in years. The numbers on the curves refer to corresponding legends the chart. The elephant, like the horse, was measured in standing position.

TABLE 4.—LIVE WEIGHT, RESTING AND BASAL METABOLISM OF JERSEY CATTLE FEMALES AT DIFFERENT AGES

Age Mos.	Live Weight kgs.	Metabolism, Cal./kg./day		Metabolism, Cal./day	
		Resting	Basal	Resting	Basal
2	44.0	48.2	36.5	2121	1606
4	73.0	42.6	32.2	3110	2351
6	111	37.9	28.7	4207	3186
8	146	34.1	25.8	4979	3767
10	174	30.9	23.5	5377	4072
12	201	28.4	21.5	5708	4322
14	228	26.3	19.8	5974	4514
16	256	24.3	18.4	6221	4710
18	283	22.9	17.3	6481	4896
20	310	21.7	16.4	6727	5084
22	338	20.7	15.7	6997	5307
24	366	19.9	15.1	7283	5527
26	396	19.2	14.5	7603	5742
28	404	18.7	14.2	7553	5737
30	404	18.2	13.8	7353	5575
32	406	17.8	13.5	7227	5481
34	416	17.5	13.0	7280	5491
36	434	17.2	13.0	7465	5642
38	456	17.0	12.9	7752	5882
40	480	16.8	12.7	8064	6096

$$Q/m = 39e^{-.008t} + 16$$

$$Q_b/m = Q/m - (Q/m \times 0.243)$$

TABLE 5.—LIVE WEIGHT, RESTING AND BASAL METABOLISM OF JERSEY CATTLE MALES AT DIFFERENT AGES

Age Mos.	Live Weight kgs.	Metabolism, Cal./kg./day		Metabolism, Cal./day	
		Resting	Basal	Resting	Basal
2	47.0	48.8	36.1	2294	1697
4	80.0	43.0	31.8	3440	2544
6	120	38.3	28.3	4596	3396
8	155	34.4	25.5	5332	3953
10	193	31.3	23.2	6041	4478
12	232	28.8	21.3	6682	4942
14	270	26.7	19.8	7209	5346
16	310	25.1	18.6	7781	5766
18	345	23.7	17.5	8177	6038
20	377	22.6	16.7	8520	6296
22	410	21.8	16.1	8938	6601
24	435	21.0	15.5	9135	6743

$$Q/m = 38e^{-.105t} + 18$$

$$Q_b/m = 28.1e^{-.105t} + 13.3$$

TABLE 6.—LIVE WEIGHT, RESTING AND BASAL METABOLISM OF HOLSTEIN CATTLE FEMALES AT DIFFERENT AGES

Age Mos.	Live Weight kgs.	Metabolism, Cal./kg./day		Metabolism, Cal./day	
		Resting	Basal	Resting	Basal
2	62	41.0	31.6	2542	1959
4	100	36.9	28.4	3690	2840
6	145	33.3	25.7	4829	3727
8	186	30.4	23.4	5654	4352
10	221	27.8	21.4	6144	4729
12	255	25.6	19.7	6528	5024
14	292	23.8	18.3	6950	5344
16	330	22.4	17.3	7392	5709
18	367	21.1	16.3	7744	5982
20	403	20.0	15.4	8060	6206
22	440	19.0	14.6	8360	6424
24	483	18.3	14.1	8639	6810
26	524	17.6	13.6	8922	7126
28	544	17.0	13.1	9248	7126
30	509	16.6	12.8	8449	6515
32	490	16.2	12.5	7938	6125
34	508	15.8	12.2	8026	6198
36	520	15.6	12.0	8112	6240
38	536	15.3	11.8	8201	6325
40	553	15.1	11.6	8350	6415

$$Q/m = 32e^{-.084t} + 14$$

$$Q_b/m = Q/m - (Q/m \times 0.229)$$

TABLE 7.—LIVE WEIGHT, RESTING AND BASAL METABOLISM OF SHEEP FEMALES AT DIFFERENT AGES

Age Mos.	Live Weight kgs.	Metabolism, Cal./kg./day		Metabolism, Cal./day	
		Resting	Basal	Resting	Basal
2	18.5	55.3	44.9	1023	831
4	33.5	45.3	36.8	1518	1233
6	39.8	38.7	31.5	1540	1254
8	44.1	34.6	28.1	1526	1239
10	48.0	31.8	25.9	1526	1243
12	53.3	30.1	24.5	1604	1306
14	59.7	29.0	23.6	1731	1409
16	53.0	28.3	23.1	1500	1224
18	54.6	27.8	22.7	1518	1239
20	55.8	27.5	22.4	1535	1250
22	60.8	27.4	22.3	1666	1356
24	64.7	27.2	22.2	1760	1436
26	59.7	27.1	22.1	1618	1319
28	56.7	27.1	22.1	1537	1253
30	58.5	27.0	22.0	1580	1287

$$Q/m = 44e^{-.22t} + 27$$

$$Q_b/m = 35.6e^{-.22t} + 22$$

TABLE 8.—LIVE WEIGHT, RESTING AND BASAL METABOLISM OF SHEEP WETHERS AT DIFFERENT AGES

Age Mos.	Live Weight kgs.	Metabolism, Cal./kg./day		Metabolism, Cal./day	
		Resting	Basal	Resting	Basal
2	18.5	---	33.2	---	614
4	34.0	46.6	30.8	1584	1047
6	41.2	43.2	28.7	1780	1182
8	45.8	40.1	26.8	1837	1227
10	51.0	37.4	25.1	1907	1280
12	58.3	35.1	23.7	2046	1382
14	65.0	33.0	22.4	2145	1456
16	69.7	31.1	21.3	2168	1485
18	74.0	29.5	20.3	2183	1502
20	78.2	28.0	19.4	2190	1517
22	83.1	26.7	18.6	2219	1546
24	87.7	25.6	17.9	2245	1570
26	89.7	24.6	17.4	2207	1561
28	84.9	23.7	16.8	2012	1426
30	90.9	22.9	16.4	2082	1491

$$Q/m = 38e^{-.069t} + 17$$

$$Q_b/m = 23e^{-.069t} + 13$$

TABLE 9.—LIVE WEIGHT, RESTING AND BASAL METABOLISM OF BEEF FEMALES AT DIFFERENT AGES

Age Mos.	Live Weight kgs.	Metabolism, Cal./kg./day		Metabolism, Cal./day	
		Resting	Basal	Resting	Basal
4	87	40.1	23.7	3489	2062
6	130	35.4	22.1	4602	2873
8	174	31.5	20.8	5481	3619
10	214	28.4	19.6	6078	4194
12	247	25.7	18.7	6348	4619
14	280	23.6	17.9	6608	5012
16	317	21.9	17.3	6942	5484
18	351	20.4	16.7	7160	5862
20	383	19.3	16.3	7392	6243
22	399	18.3	15.9	7302	6344
24	416	17.5	15.6	7280	6490
26	452	16.9	15.3	7639	6916
28	444	16.3	15.1	7237	6704
30	417	16.0	14.9	6672	6213
32	414	15.6	14.8	6458	6127
34	423	15.3	14.6	6472	6176
36	435	15.1	14.5	6569	6308
38	450	14.9	14.4	6705	6480
40	454	14.7	14.4	6674	6538
42	456	14.6	14.3	6658	6521

$$Q/m = 39e^{-.10t} + 14$$

$$Q_b/m = 14e^{-.091t} + 14$$

TABLE 10.—LIVE WEIGHT, RESTING AND BASAL METABOLISM OF BEEF STEERS AT DIFFERENT AGES

Age Mos.	Live Weight kgs.	Metabolism, Cal./kg./day		Metabolism, Cal./day	
		Resting	Basal	Resting	Basal
4	116	36.3	27.6	4211	3203
6	172	32.1	24.4	5521	4197
8	228	28.7	21.8	6544	4970
10	280	26.0	19.8	7280	5544
12	336	23.8	18.1	7997	6082
14	384	22.1	16.8	8486	6451
16	433	20.7	15.8	8963	6841
18	483	19.6	15.0	9467	7245
20	530	18.7	14.3	9911	7579
22	575	17.9	13.7	10293	7878
24	622	17.1	13.2	10761	8210
26	665	16.9	12.9	11239	8579
28	706	16.5	12.6	11649	8896
30	745	16.2	12.4	12069	9238
32	781	16.0	12.2	12496	9528
34	810	15.8	12.1	12798	9801
36	840	15.6	11.9	13104	9996
38	865	15.5	11.8	13408	10207
40	888	15.4	11.8	13675	10478

$$Q/m = 33e^{-.11t} + 15$$

$$Q_b/m = 25e^{-.11t} + 11.5$$

TABLE 11.—LIVE WEIGHT, RESTING AND BASAL METABOLISM OF HORSES, FEMALES AND GELDINGS COMBINED, AT DIFFERENT AGES

Age Mos.	Live Weight kgs.	Metabolism, Cal./kg./day		Metabolism, Cal./day	
		Resting	Basal	Resting	Basal
2	166	37.9	28.7	6291	4764
4	247	30.7	25.9	7583	6397
6	297	26.8	23.6	7960	7009
8	336	24.6	21.7	8266	7291
10	369	23.5	20.2	8672	7454
12	400	22.8	18.9	9120	7560
14	426	22.4	17.9	9542	7625
16	446	22.2	17.0	9901	7582
18	457	22.1	16.3	10100	7449
20	469	22.1	15.7	10365	7363
22	482	22.0	15.2	10604	7326
24	507	22.0	14.8	11154	7504
26	544	22.0	14.5	11968	7888
28	576	22.0	14.3	12672	8237
30	607	22.0	14.0	13354	8498
32	632	22.0	13.9	13904	8785
34	660	22.0	13.7	14520	9042
36	649	22.0	13.6	14278	8826
38	635	22.0	13.5	13970	8573
40	658	22.0	13.4	14476	8817

$$Q/m = 29e^{-.30t} + 22$$

$$Q_b/m = 19e^{-.097t} + 13$$

TABLE 12.—LIVE WEIGHT, RESTING AND BASAL METABOLISM OF SWINE FEMALES AT DIFFERENT AGES

Age Mos.	Live Weight Kgs.	Metabolism, Cal./kg./day		Metabolism, Cal./day	
		Resting	Basal	Resting	Basal
2	8.0	118.1	48.6	945	389
4	23	80.6	37.3	1853	858
6	55	57.1	29.6	3141	1628
8	94	42.1	24.4	3957	2294
10	126	32.6	20.7	4108	2608
12	152	26.6	18.3	4043	2782
14	173	22.9	16.6	3962	2872
16	194	20.5	15.5	3977	3007
18	213	19.1	14.7	4068	3131
20	227	18.1	14.1	4109	3201
22	240	17.5	13.8	4200	3312
24	252	17.1	13.5	4309	3402
26	260	17.0	13.4	4420	3484
28	266	16.8	13.3	4469	3538
30	269	16.7	13.2	4492	3551
32	270	16.5	13.1	4455	3537
34	270	16.5	13.0	4455	3510
36	270	16.5	13.0	4455	3510

$$Q/m = 161e^{-.23t} + 16.5$$

$$Q_b/m = 52e^{-.19t} + 13$$

TABLE 13.—LIVE WEIGHT, RESTING AND BASAL METABOLISM OF SWINE MALES AT DIFFERENT AGES

Age Mos.	Live Weight Kgs.	Metabolism, Cal./kg./day		Metabolism, Cal./day	
		Resting	Basal	Resting	Basal
2	7.0	86.0	50.8	602	356
4	20	66.7	39.6	1334	792
6	47	53.0	32.2	2491	1513
8	74	43.5	27.3	3219	2020
10	98	36.7	24.1	3597	2362
12	118	31.8	22.0	3752	2596
14	139	28.5	20.6	3962	2863
16	159	26.2	19.7	4166	3132
18	177	24.5	19.1	4337	3381
20	195	23.3	18.8	4544	3666
22	212	22.4	18.5	4749	3922
24	228	21.9	18.3	4993	4172
26	244	21.5	18.2	5246	4441
28	258	21.1	18.2	5444	4696
30	273	21.0	18.1	5733	4941

$$Q/m = 93e^{-.176t} + 20.5$$

$$Q_b/m = 50e^{-.21t} + 18$$

TABLE 14.—LIVE WEIGHT, RESTING AND BASAL METABOLISM OF DEIGHTON'S SWINE AT DIFFERENT AGES

Age Mos.	Live Weight Kgs.	Metabolism, Cal./kg./day		Metabolism, Cal./day	
		Resting	Basal	Resting	Basal
2	12	75.1	---	223	---
4	24	61.4	34.8	901	---
6	42	50.7	30.6	1474	835
8	60	42.5	27.1	2129	1285
10	78	36.3	24.2	2550	1626
12	96	31.4	21.7	2831	1888
14	114	27.6	19.8	3014	2083
16	131	24.8	18.1	3146	2257
18	149	22.5	16.8	3249	2371
20	164	20.8	15.6	3353	2503
22	177	19.4	14.6	3411	2558
24	189	18.4	13.9	3434	2584
26	200	17.7	13.2	3478	2627
28	211	17.0	---	3540	2640
30	220	16.6	---	3587	---
				3652	---

$$Q/m = 78e^{-.13t} + 15$$

$$Q_b/m = 36e^{-.093t} + 10$$

TABLE 15.—LIVE WEIGHT, RESTING AND BASAL METABOLISM OF HOLSTEIN CATTLE MALES AT DIFFERENT AGES

Age Mos.	Live Weight Kgs.	Metabolism, Cal./kg./day		Metabolism, Cal./day	
		Resting	Basal	Resting	Basal
2	71	42.9	---	3046	---
4	112	37.6	---	4211	---
6	166	33.0	---	5478	---
8	226	28.9	---	6531	---
10	280	25.3	---	7084	---
12	333	22.2	---	7393	---
14	380	19.5	---	7410	---

$$Q/m = 49e^{-.066t}$$

DISCUSSION, SUMMARY AND CONCLUSIONS

This bulletin presents data and discussions on resting and basal energy metabolism per unit weight as a function of *age*, in the same manner as the preceding paper (Missouri Research Bulletin 166) presented data on resting and basal energy metabolism as a function of *live weight*.

The same exponential equations may be used to represent the metabolism as a function of age or of live weight; but the agreement between observed and computed values is better when metabolism is expressed as a function of weight alone than of age alone, as weight influences metabolism to a much greater extent than does age.

We are not yet able to report quantitative evaluations of the relative influences of body weight and of age on energy metabolism during active growth, on account of the difficulty of investigating experimentally each of these factors independently. It appears, however, that when immature rats are kept at a constant body weight for a long period, then their metabolism also remains practically constant. In other words, whatever the influences of increasing age on the course of metabolism per unit weight of immature animals, they are relatively slight as compared to the influence of increasing live weight on metabolism per unit weight. This conclusion may also be deduced from the fact that during adulthood, that is, when live weight naturally remains practically constant, the decline in metabolism with increasing age is very slight as compared to the decline during normal growth when live weight increases rapidly.

The cause of the decreasing basal metabolism per unit weight with increasing live weight will probably be found in the fact that the several organs and tissues of the body differ in their metabolic intensity under basal conditions; and that the greater the live weight of an organism, the smaller in proportion is the quantity (or possibly activity, as pulse rate) of the most actively metabolising organs under basal conditions. It may well be that the visceral organs and tissues are the most active under *basal* conditions; and therefore the metabolism per unit weight is mainly a function of the relative mass of these organs in the body. The idea seems reasonable in view of the fact that under conditions of basal metabolism the adipose, muscular, and skeletal systems, which constitute the bulk of the live weight, are relatively quiescent, while the visceral organs are perhaps no less active under basal than under other conditions. Metabolism is more nearly proportional to area than to live weight, probably because the ratio of area to live weight tends to vary in the same manner as the ratio of the visceral organs to live weight (see Fig. 1c). This concept is in general agreement with the popular ideas that a heavy animal carries much "dead"

weight; that beyond a certain age, weight is a liability, as it is a strain on the vital organs to support the masses of the relatively nonessential muscular, fatty, and skeletal tissues; that those engaging in competitive sports requiring great physical exertion must keep their body weights at a minimum. There are essential organs or tissues, and there are relatively non-essential organs or tissues which are supported by the essential organs; and the intensity of metabolism under basal conditions is largely a function of the essential (visceral, nervous, endocrine) organs rather than of live weight. Hence, the justification of referring metabolism to "active mass" rather than to live weight, or even to surface area. True, we have no good measure of "active mass"; but this will, no doubt, come in due time.

By way of summary, it may be said that from a practical point of view, the data constitute the essential contribution of this bulletin. We know now, as we have not known before, how the energy metabolism changes with age in farm animals, not only *basal* metabolism—which is an unusual condition in farm animals—but also that which seems to us more important, *resting* metabolism, which is the average heat production of quietly resting animals under normal conditions of food supply. These data cover the periods of gestation and lactation. The inclusion of a large number of species during growth in this study constitutes a contribution towards the evaluation of the relative efficiencies of growth in different species; while the inclusion of a large number of individuals in each species constitutes a contribution towards the evaluation of individual differences in efficiency of growth. The metabolism data on immature animals held at a constant body weight will contribute towards our knowledge of maintenance cost for energy of young animals distinct from energy requirements for growth.

From a theoretical point of view, in addition to the above, this bulletin is a contribution towards the subjects of comparative metabolism, and of comparative growth and development; also towards a search for rational units of reference for expressing metabolic rates, not only for adults, but also for growing animals.

REFERENCES CITED

- Benedict, F. G., Basal Metabolism Data on Normal Men and Women (Series II) with Some Considerations on the Use of Prediction Standards. *Am. J. Physiol.*, 1928, 85, 607.
- Age and Basal Metabolism of Adults. *Am. J. Physiol.*, 1928, 85, 650.
- and MacLeod, G., The Heat Production of the Albino Rat. II. Influence of Environmental Temperature, Age, and Sex; Comparison with the Basal Metabolism of Man. *J. Nutrition*, 1929, 1, 367.
- and Petrik, J. M., Metabolism Studies on the Wild Rat. *Am. J. Physiol.*, 1930, 94, 662.
- and Ritzman, E. G., Über die den Energieumsatz bei Schafen beeinflussenden Faktoren. *Arch. Tierernahrung u. Tierzucht, Abt. B.*, 1931, 1, 1. See also Ritzman, E. G., and Benedict, F. G., The Energy Metabolism of Sheep. *Univ. New Hampshire, Agric. Expt. Sta., Tech. Bull.* 43, 1930; The Heat Production of Sheep Under Varying Conditions. *Id.*, *Tech. Bull.* 45, 1931.
- and Talbot, F. B., Metabolism and Growth from Birth to Puberty. *Pub. 302, Carnegie Institution of Wash.*, 1921.
- and Meyer, M. H., The Basal Heat Production of Elderly Women. *Proc. Am. Philos. Soc.* 1932, lxxi, 143.
- Boothby, W. M., and Sandiford, I., *J. Biol. Chem.*, 1922, 54, 791.
- Deighton, T. A., A Study of the Metabolism of Two Breeds of Pig. *J. Agric. Sc.*, 1929, xix, 140.
- Donaldson, H. H., *The Rat. Data and Reference Tables.* Philadelphia, 1924.
- DuBois, E. F., *Basal Metabolism in Health and Disease,* Philadelphia, 1927.
- Ginglinger, A., and Kayser, C., Etablissement de la thermo-régulation chez les homéothermes au cours du développement, *Ann. physiologie et de physico-chimie Biologique*, 1929, p. 710.
- Harris, J. A., and Benedict, F. G., A Biometric Study of Basal Metabolism in Man. *Carnegie Inst. Wash.*, *Pub. No.* 279, 1919.
- Hicks, C. S., Matters, R. F., and Mitchell, M. L., The Standard Metabolism of Australian Aborigines. *Australian J. Experimental Biology and Medical Science*, 1931, viii, 69.
- Latimer, H. B., Postnatal Growth of the Body, Systems, and Organs of the Single-Comb White Leghorn Chicken. *J. Agric. Res.*, 1924, xxix, 363.
- Lusk, G., *The Science of Nutrition.* Philadelphia, 1928 (fourth edition).
- and Du Bois, E. F., On the Constancy of the Basal Metabolism. *J. Physiol.*, 1924, lix, 213.
- Mayer, A., and Nichita, G., Sur les échanges des Homéothermes au cours du réchauffement-contributions à l'étude du "métabolisme minimum" et de la thermogénèse. *Ann. Physiol. et de physico-chim. Biolog.*, 1929, v, No. 1; sur une adaption du lapin aux températures élevées. *Id.*, p. 609; Sur les variations du métabolisme du lapin après exposition au froid, variation saisonnière du métabolisme du lapin et modification de la fourrure. *Id.*, p. 621.
- McKay, H., Basal Metabolism of Women over Thirty-five Years of Age. *Ohio Agric. Exper. Station*, 1932, *Bull.* 497, pp. 145-6 (in 50th annual report of the station).
- Mitchell, H. H., Card, L. E., and Haines, W. T., The Effect of Age, Sex, and Castration on the Basal Heat Production of Chickens. *J. Agric. Res.*, 1927, 34, 945.
- Card, L. E., and Hamilton, T. S., The Growth of White Plymouth Rock Chickens. *Univ. Ill. Agric. Expt. Sta. Bull.* 278, 1926. A Technical Study of the Growth of White Leghorn Chickens. *Univ. Ill., Agric. Expt. Station*, 1931, *Bull.* 367.
- and Carman, G. G., Effect of Excessive Amounts of Vitamine B on the Basal Metabolism of Rats of Different Ages. *Am. J. Physiol.*, 1926, lxxvi, 385.
- and Haines, W. T., The Basal Metabolism of Mature Chickens and the Net-energy Value of Corn. *J. Agric. Res.*, 1927, 34, 927.
- Moulton, C. R., Trowbridge, P. F., and Haigh, L. D., Studies in Animal Nutrition. II. Changes in Proportions of Carcas and Offal on Different Planes of Nutrition. *Univ. Missouri. Agric. Expt. Sta.*, 1922, *Res. Bul.* 54.
- Needham, J., *Chemical Embryology.* Cambridge (England), 1931, (3 volumes).

- Rapkine, L., *Energétique du développement de l'oeuf d'après les travaux récents*. Paris, 1928. (Published by A. Chabine, 7 rue de conde).
- , *L'énergétique du développement de l'oeuf*. Arch. d'Anatomie microscopique 1929, xxv, 482.
- Riddle, O., Smith, —, and Benedict, F. G., Personal Communication of Jan. 16, 1932, including data presented in (1), (2), and (3) Figure 9.
- , Charles, D. R., and Cauthen, G. E., Relative Growth Rates in Large and Small races of Pigeons. Proc. Soc. Exper. Biology and Med., 1932, xxix, 1216.
- , Christman, G., and Benedict, F. G., Differential Response of Male and Female Ring Doves to Metabolism Measurements at Higher and Lower Temperatures. Am. J. Physiol., 1930, 95, 111.
- , Nussmann, T. C., and Benedict, F. G., Metabolism During Growth in a Common Pigeon. Am. J. Physiol., 1932, 101, 251.
- , Smith, G. C., and Benedict, F. G., The Basal Metabolism of the Mourning Dove and Some of its Hybrids. Am. J. Physiol., 1932, 101, 260.
- Schmalhausen, I., Studien über Wachstum und Differenzierung. III. Die Embryonale Wachstums kurve des Hünchens. Arch. Entwicklunsmech. d. Organismen, 1926, 108, 322.
- , Beiträge zur quantitativen analyse der Formbildung. I. Über die gesetzmässigkeiten des embryonalen Wachstums. Arch. Entwicklungsmechanik d. organismen, 1927, 109, 31.
- Terroine, E., et Wurmser, R., L'énergie de croissance. I. Le développement de *Aspergillus niger*. Bull. Soc. Chimie Biologique, 1922, iv, 519.
- Wurmser, René, Oxydations et Réductions. Paris, 1930. (Published by Les Presses Universitaires de France).
- Zuntz, N., and Loewy, A., Einfluss der Kriegskost auf den Stoffwechsel nach Selbst beobachtungen. Berl. klin. Wochenschr., 1916, liii, 826; Biochem. Z., 1918, xc, 244.