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GROWTH AND DEVELOPMENT

*With Special Reference to Domestic Animals**

XI. Further Investigations on Surface Area With Special
Reference to Its Significance in Energy Metabolism

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GROWTH AND DEVELOPMENT

With Special Reference to Domestic Animals

XI. Further Investigations on Surface Area With Special Reference to Its Significance in Energy Metabolism

SAMUEL BRODY, JAMES E. COMFORT, JOHN S. MATTHEWS

PREFATORY NOTES AND ACKNOWLEDGMENTS

This bulletin includes *surface integrator* measurements of surface area of 482 dairy cattle, 341 beef cattle, 11 horses, 16 swine. (The surface integrator and the method of its use are described in Research Bulletin 89 of this Station.) The original data cards include the following entries: age, height, condition of fleshiness, area, weight, height at withers, circumference of chest, distance from shoulder to hips, width of hips. For financial reasons, it is not practicable to publish the numerical data. For the use of those who may desire to examine the original data, the data cards will be kept on file at the Missouri Agricultural Experiment Station.

The dairy cattle were measured by J. S. Matthews under the supervision of Professor A. C. Ragsdale. The beef cattle, horses, and swine were measured by J. E. Comfort under the supervision of Professor E. A. Trowbridge. Professor D. W. Chittenden cooperated with the measurements of the horses.

A portion of the expenses involved in this work was paid from a grant of the National Research Council for the National Live Stock and Meat Board Fellowship Fund. Grateful acknowledgment is made to the Council and to the Chairman of the Committee of National Live Stock and Meat Board Fellowships, National Research Council, for recommending the grant for this and related work in growth of domestic animals.

ABSTRACT

1. Data are presented on the relation of surface area to body size of 482 dairy cattle (189 Holsteins, 154 Ayrshires, 96 Jerseys, 43 Guernseys); on 341 beef cattle (Shorthorns, 145 females, 54 males, 20 steers; Herefords, 69 females, 38 males, 7 steers; Angus, 8 steers), on 11 horses, and on 16 swine.

2. A mathematical (graphical) analysis is presented of these original data, as well as of the available published data on the relation of area to body size and on the relation of heat production to body size.

3. It is shown that the numerical value of the power in the power function relating surface area to body weight varies from about 0.4 to about 0.7 depending on the relative variations in the linear size of the animals as compared to variations in body weight. In this connection the formulæ of Meeh, of Du Bois and Du Bois, and of Cowgill and Drabkin are subjected to critical analysis; as is also the so-called Surface Area Law of Rubner. It is concluded, on mathematical and on biological grounds, that while it may be more convenient, and perhaps more enlightening, to relate heat production to surface area, it is simpler to relate heat production directly to body size raised to some power by a method explained in detail in the text.

I. FORMULAE RELATING SURFACE AREA TO BODY SIZE, WITH SOME APPLICATIONS

This bulletin is a continuation of Missouri Research Bulletin 89 to which the reader is referred for the introductory notes.

Perhaps we had better state at the outset that we shall make much use of the following equations

$$A = CH^mW^n \quad (1)$$

or

$$E = CH^mW^n$$

and

$$A = CW^n \quad (2)$$

or

$$E = CW^n$$

in which A is surface area and E is heat production for body weight W , and height H .

Equations (1) and (2) are closely related, for if in equation (1), $m = 0$, then $H^m = 1$, and equation (1) becomes equation (2).

Equation (2), known to the mathematician as a *power function*, was used by Meeh (1879) to represent the relation between surface area and weight in man. Meeh assigned the value $\frac{2}{3}$ to n in equation (2) on the basis of the assumption that the areas of bodies of similar shape are directly proportional to the squares of their linear size, and the volumes are directly proportional to the cubes of their linear size. When $n = \frac{2}{3}$, equation (2) is known as the Meeh surface-area formula.

Du Bois criticised the Meeh formulae in its application to man in the following words: "It is obvious that a tall, thin man may have exactly the same weight as a short, fat man, yet have a much larger surface area." This objection finally led Du Bois and Du Bois (1916) to adopt equation (1) thus taking into consideration the height as well as the weight of the individual. Equation (1) is for this reason often spoken of as the Du Bois height-weight formula, that is, when m is taken to have the value 0.725, and $n = 0.425$.

Briefly, Du Bois and Du Bois (1915) employed the following reasoning in arriving at the numerical values of m and n for man: Since area is a bidimensional measurement, it follows that in the equation relating area to size, the formula must be bidimensional on both sides of the equation. Since length is a unidimensional measurement, and weight is a tridimensional measurement, the equations

$$A = CW^{1/3}H \quad (3)$$

and

$$A = CW^{1/2}H^{1/2} \quad (4)$$

may be given as examples of formulae which are bidimensional on both sides. Equations (3) and (4) were investigated for this purpose using the *actually* measured (by the mold method) areas of nine subjects, and the computed (by the "linear formula") areas of 33 subjects by solving for the constant, C , the values of m and n being assumed as in equations (3) and (4).

Since equations (3) and (4) were found to give errors opposite in sign, other values of the exponents between the two sets given in equations (3) and (4) were tried. In order to keep the formula bidimensional, it was put in the form

$$A = CW^{1/a} H^{1/b} \quad (5)$$

and care taken that the sum of $1/a$ and $1/b$ remained 2 as in equations (4) and (5). After trying several combinations of a and b , Du Bois and Du Bois concluded that the best agreements between observed and computed values are obtained when $a = 2.35$ and $b = 1.38$. The final equation of Du Bois and Du Bois (1916) is therefore,

$$\begin{aligned} A &= CW^{1/2.35} H^{1/1.38} \\ &= CW^{.425} H^{.725} \end{aligned} \quad (6)$$

The average value of C was found to be 71.84. The well-known Du Bois prediction chart was then prepared on the basis of equation (6).

Cowgill and Drabkin (1927) concluded that in equation (1) $m = 1$. They arrived at this conclusion by the following reasoning. They related area to the product of body weight and a correction factor for body build (or state of nutrition) by the formula

$$A = CW^n \frac{N_m}{N_{obs}} \quad (7)$$

in which A is surface area for weight W , and the nutritional state $\frac{N_m}{N_{obs}}$. N_m represents the ratio of the cube root of weight to the linear measurement (that is, of $\frac{W^{1/3}}{L}$) for the most obese individual observed. N_{obs} represents this ratio for the animal under consideration.

In the words of these authors, formula (7) "is essentially the Meeh-Rubner expression multiplied by a factor correcting for the nutritive state of the subject. The principle upon which this factor is based is the same as that employed by von Pirquet (1917) in arriving at his *pelidisi*. For unit increases in length (sitting height or stem length) there is unit expansion in the three dimensions which determine volume. If specific gravity is assumed to be constant, weight instead of volume may be taken as the factor with which to compare length. Inasmuch as weight is a function of three dimensions, the cube root of weight is the proper unit with which to compare unit change in length. It is obvious that the value of the ratio should be practically constant in subjects of the same species of approximately the same age and characterized by the same nutritive states. It is also obvious that the values for this ratio will be higher in obese individuals than in thin subjects."

The value of the exponent of W , namely 0.70, was arrived at by a method of trial.

Cowgill and Drabkin point out that while their formula, equation (7), can be simplified to yield the power function (1) (in which case $m = 1$), it is preferable to write the formula in the form of equation (7) "because of this advantage: its character as a combination of Meeh-Rubner-Dreyer ideas with a correction factor for the nutritive state of the subject is thus made apparent."

It is evident that the proposed equations of Meeh, of Du Bois and Du Bois, and of Cowgill and Drabkin may all be reduced to the generalized equation (1). In Meeh's formula, the value of m in (1) is zero; in Cowgill and Drabkin's formula, the value of m in (1) is 1; in the formula of DuBois and Du Bois, m in (1) is .725.

After reading these papers, the first problem that called for solution is the evaluation of m in equation (1); is it 0, 1, or .725?

The solution of the problem is embodied in Fig. 1. This figure was prepared on the basis of the following considerations.

Equation (1) may be written in the form

$$\frac{A}{H^m} = CW^n \quad (8a)$$

Taking logarithms, we obtain the equation

$$\log \frac{A}{H^m} = n \log W + \log C \quad (8b)$$

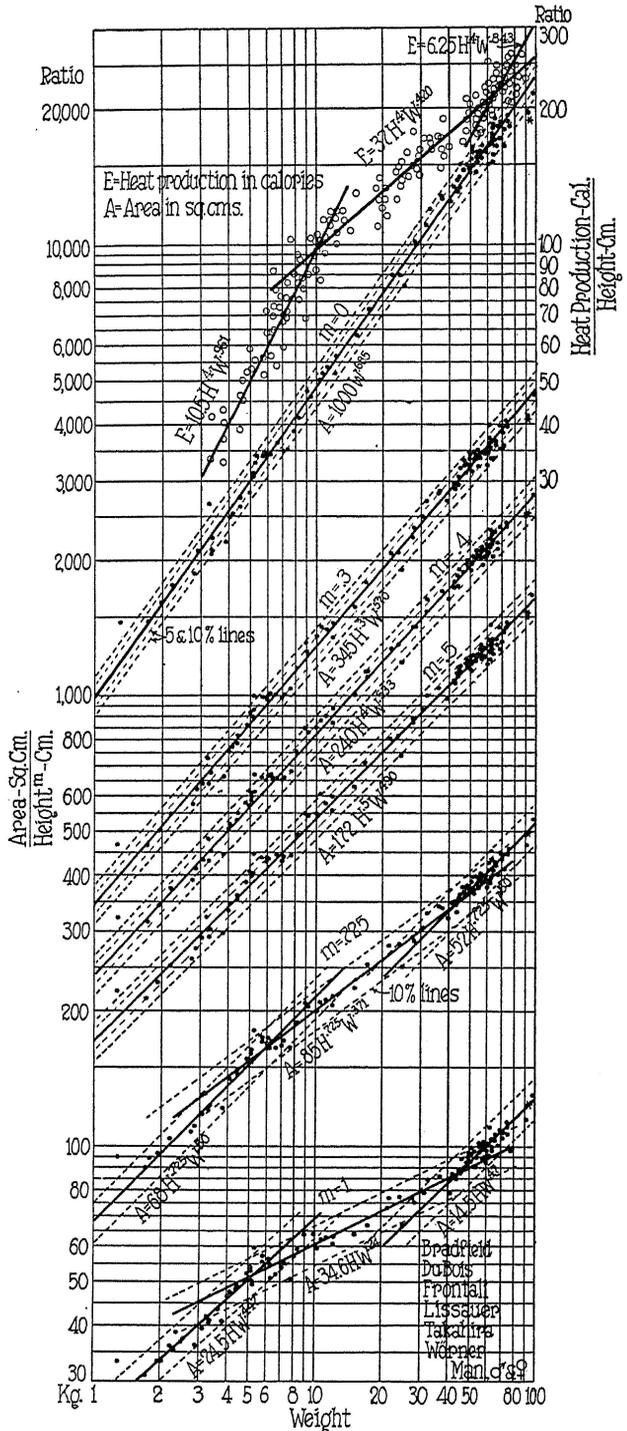
which indicates that plotting the logarithms of the ratios of area to height, raised to the power m , against the logarithms of weight, should give a straight line of slope n . It is these ratios for different values of m that are represented in Fig. 1.

The lowest curve in Fig. 1 represents the ratios of area to height (that is, $m = 1$) plotted against weight on a logarithmic grid (equivalent to plotting $\log \frac{A}{H}$ against $\log W$). The curve is seen to be made up of three fairly distinct segments. The equations for each of the three segments are given on the curve. Since according to equation (1), the plot of $\log \frac{A}{H^m}$ against W should result in a straight line while Fig. 1 shows that it is not a straight line; therefore, either equation (1) does not represent the data, or the value of m is not 1; in other words this curve rules out the value of m as assumed by Cowgill and Drabkin.

The second curve from the bottom represents a similar plot when $m = .725$ (i. e., the value of m as assumed by Du Bois and Du Bois). When the value of m is 0.725, the distribution of the data points approaches more nearly a straight line; but it is not straight; that is to say, the value of 0.725 (assumed by Du Bois and Du Bois) is too high.

In similar manner we assumed the value of m to be .5, .4, .3, and 0, and the resulting values of $\frac{A}{H^m}$ were plotted against W . Looking over the chart we concluded by *inspection* that the best agreement between observed and computed values is obtained when $m = 0.4$. We included in these computations the data by Bradfield (1927), Du Bois and Du Bois (1915), Frontali (1927), Lissauer (1903), Takahira (1925), and Wörner

Fig. 1.—The relation between surface area, A, body weight, W, and standing height, H, in man. Also the relation between heat production, E, to W and H. The ratios of area to height, H, raised to different powers, M, are plotted against weight, W. Note, that for area, A, the straightest line is obtained when the value of the power, M, is 4. When the value of the exponent, M, is increased, the curve tends to break up into three segments. These breaks are quite distinct when the exponent, M, is 1 (value used by Cowgill and Drabkin) and .725, (value used by Du Bois). Note also that while for area, A, a straight line is obtained when the exponent of height is 4, no such straight line is obtained for the heat production curve. The star represents Mrs. McK (See Du Bois and Du Bois) weighing 204 pounds and having the height of a 12-year-old girl. Note that while the exponent of height is 1, or .7, it is below the line in the other curves. But when the exponent is 1. or .7, a straight line can not be used to represent the normal data. Note that when the exponent, M, equals zero, that is, when the height datum is not used at all, data points are distributed about a tolerably straight line.



(1923); a total of 133 measurements, and with two exceptions, all the data points are within the 10 per cent of the average. This is satisfactory considering that the data of Lissauer included dead infants in very emaciated condition.

Incidentally one can determine whether heat production is directly proportional to surface area during growth by merely plotting the ratios of heat production to height raised to the power 0.4 against weight. If heat production were proportional to surface area, during growth, then the resulting curve would have the same slope as the curve representing the plot of the ratios of area to height raised to the power 0.4. The curve for heat production is shown by the uppermost set of data (open circles). The data were taken from Benedict and co-workers (Carnegie publications 279 and 302) including all the data for males. It appears that the curves for heat production and for area are not parallel: the heat production per unit area changes with increasing weight during the period of growth. But this is well known.

The results in Fig. 1 lead to the conclusion that for individuals of "normal" build the equation relating area to weight and to height is

$$A = 240 H^{.43} W^{.53} \tag{9}$$

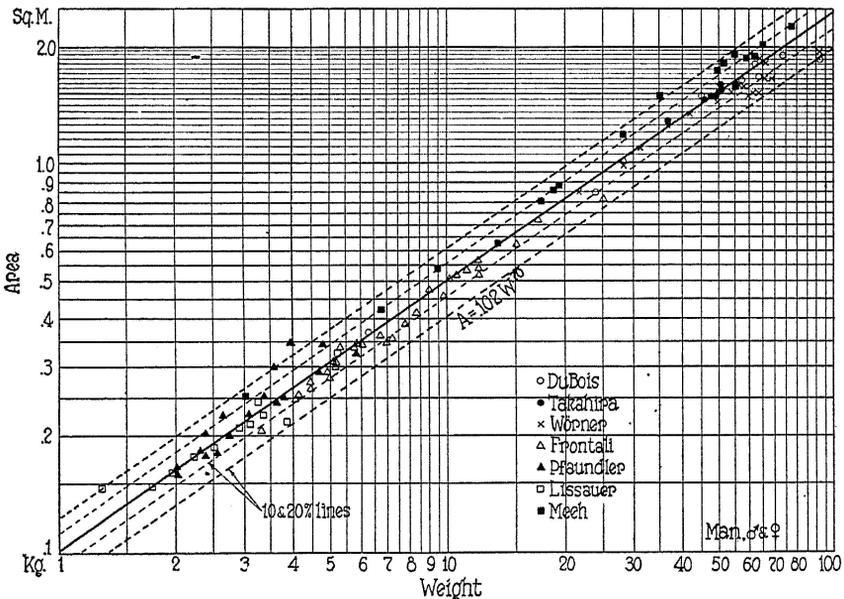


Fig. 2.—The relation between surface area and weight when the data by Meeh and Pfundler are included. By including these data the deviations from the average were increased from 10 to 20 per cent (Fig. 1). The numerical values of the constants were increased somewhat. Compare to Fig. 1 for curve $m = 0$.

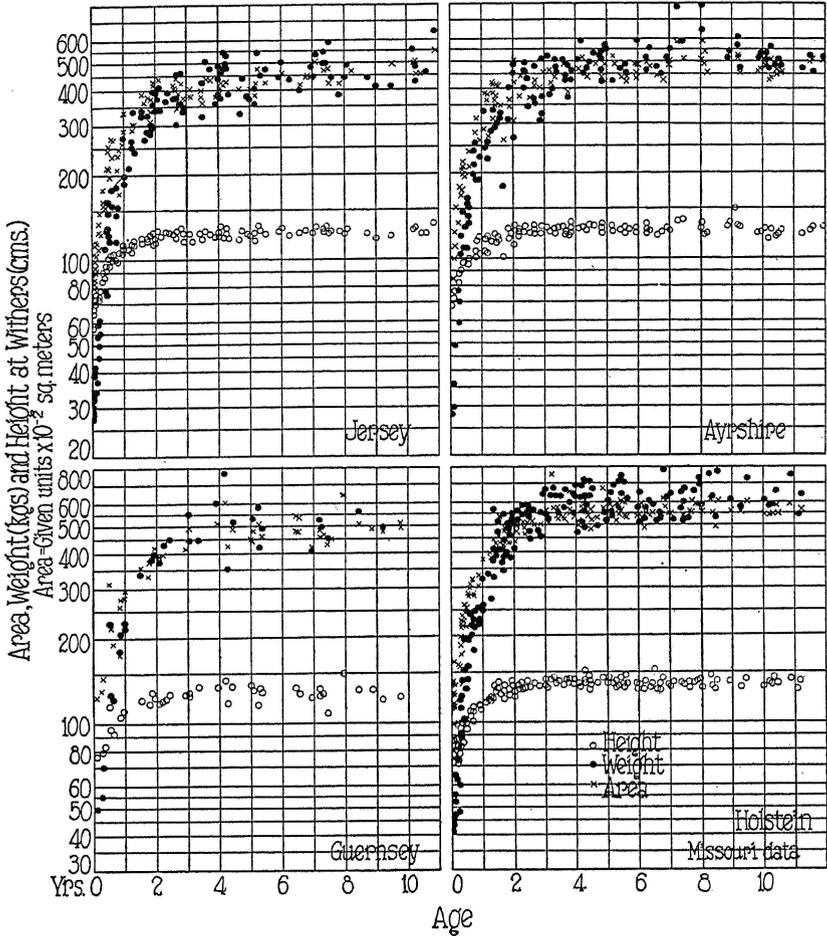


Fig. 3.—The relative increase in height at withers, body weight, and surface area (the data are plotted on an arithlog grid). The relatively small post-natal increase in linear size of the species explains the fact that the exponent for weight in the relation between area and weight is much smaller for cattle than for man; it also suggests the idea that it is not as important to have a height datum in the formula relating area to body size in cattle as it is in man. (For the relative increase in weight and in height in man during growth, See Figs. 11a and 11b, Res. Bul. 104.)

in which A is surface area in square centimeters, H height in centimeters, and W weight in kilograms.

In individuals of a normal build, it is not absolutely necessary to take height into consideration. As shown in Fig. 1, the formula

$$A = 1000 W^{.685} \tag{2b}$$

represents the data in a fairly satisfactory manner, as, with two exceptions, all data points are within 10 per cent of the average values. (A is area in square centimeters for weight, W , in kilograms.) We may say

that we have not included the measurements of Meeh (1879) and of Pfaundler (1916) because their values appear to be high as compared to other measurements. This statement is indicated in Fig. 2.

It should also be pointed out that we have not given the slightest attention to the matter of bidimensionality on both sides of equations (1) and (9), as we believe that the equation relating area to body size can not be anything but purely empirical.

It seems that Du Bois and Du Bois took special pains to get the datum for Mrs. McK. (represented by a star in Fig. (1)) on their fitted curve. Now this subject had the height of an average girl of 12 years, and she weighed 93 kilograms, that is, 205 pounds! This evidently is an extremely unusual case, and it does not seem reasonable to assume that any simple formula representing the relationship for average individuals could also represent the relationship between area and size of a subject of the type of Mrs. McK.

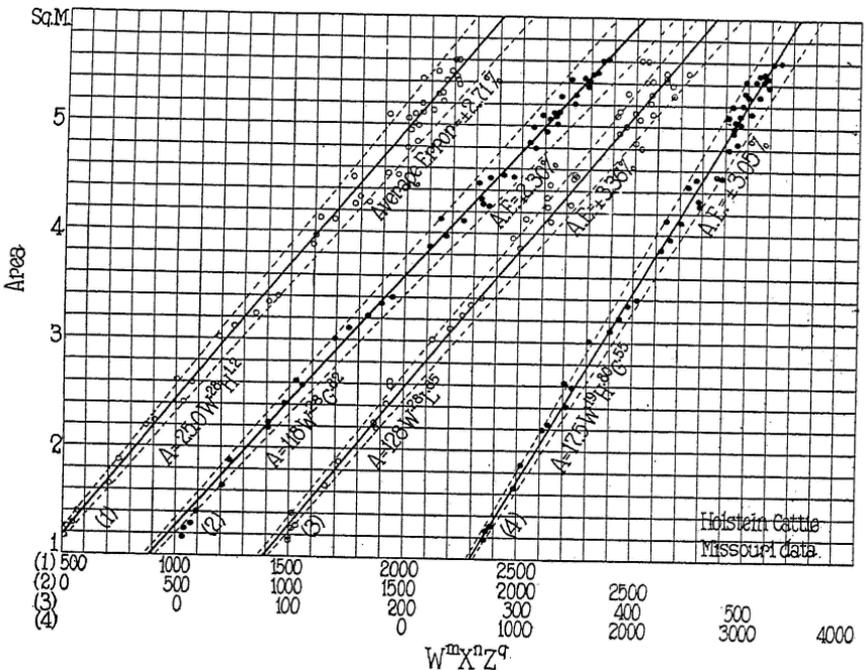


Fig. 4a.—The relation of surface area, A , to (1) weight, W , and height, H ; (2) weight and chest girth, G ; (3) weight and body length, L ; (4) weight, height, and girth. The broken lines represent 5% deviations from the average curve. Compare with Fig. 4b and note that the lowest average error, $A, E, (1.86)$ is obtained when the linear measurements are not included in the formula. In this chart the area is plotted against the products of weight, W , and several linear measurements, X, Z ; each raised to some power (m, n, q). This figure, as also the following (4b), is based on the data for Holstein cattle given in Res. Bul. 89 of this series.

Equation (2) is particularly useful for relating area to body size in domestic animals (cattle, horses, swine, sheep) during growth because the relative growth in height as compared to weight is less for animals than it is for man, and, as shown particularly in Fig. 16, introducing height as a datum in the formula by no means increases the agreement between observed and computed values. This relative amount of growth in weight and in height for man is indicated in Fig. 11b, Research Bulletin 104 of this series. The relative growth in weight and in height for cattle is indicated in Figs. 5b, 6a, and 10a, Research Bulletin 103. The relative growth in weight, height, and area is also shown in Fig. 3.

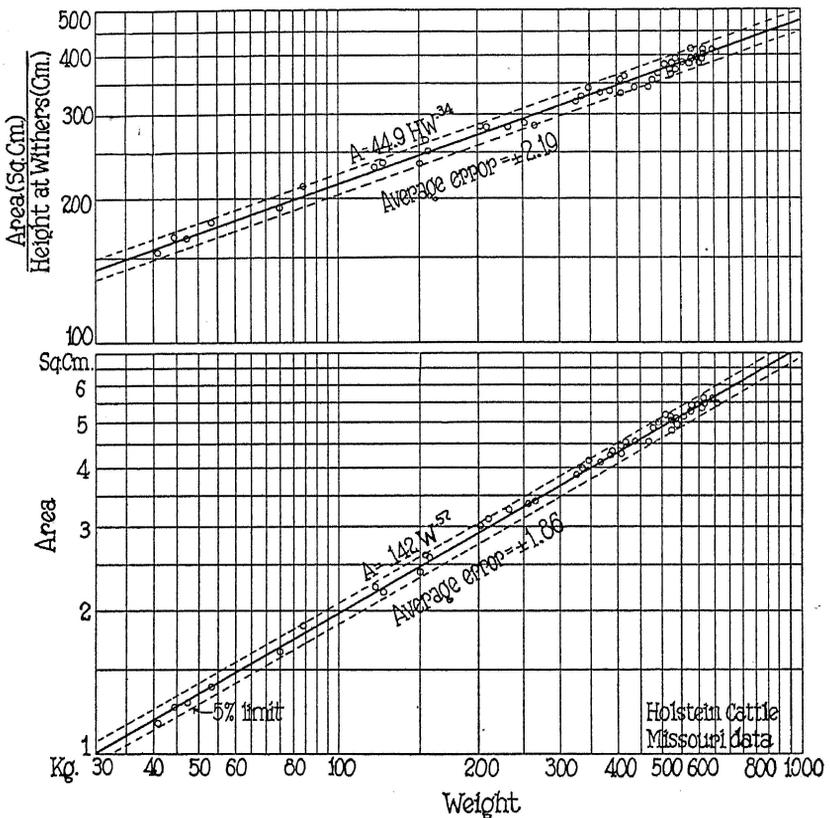


Fig. 4b.—The relation of area to weight (lower curve) and of area to weight and to height at withers (upper curve). See curve and legend in Fig. 4a.

The fact that including the height datum in the formula relating area to body size in cattle does not materially increase the agreement between observed and computed values may be shown in a more precise manner by the following considerations: Let us determine the relation

between area and any linear size, such as height at withers, body length, or chest girth by plotting area against any of these linear measurements on a logarithmic grid and by determining the constants for each linear measurement. As a matter of fact we have done this in Research Bulletin 89. The resulting equations, including equations relating area to weight, area to height, etc. may then be combined into one equation by simply dividing the exponents by a number equal to the number of equations which it is desired to combine into one equation.

Thus, in the aforementioned Research Bulletin 89 we have found the relation between area and weight for Holstein cattle to be

$$A = .142W^{.57}$$

for height at withers,

$$A = .404H^{2.4}$$

Multiplying the two, we obtain

$$A^2 = (.142W^{.57}) \times (.404H^{2.4})$$

Therefore

$$A = \sqrt{(.142W^{.57}) \times (.404H^{2.4})} = CW^{.57/2} \times H^{2.4/2}$$

If desired, the value of C may be determined empirically by plotting values for area against values of $W^{.57/2} \times H^{2.4/2}$ on arithmetically coordinate paper and determining the intercept of the resulting curve.

If we also wish to include the circumference-of-chest measurement in our formula, we divide the exponents (using the same reasoning as above) by 3. Since the relation between area and circumference of chest, G , is

$$A = 9.2G^{1.64}$$

therefore the relation of area to weight, height at withers, and circumference of chest is

$$A = CW^{.57/3} H^{2.4/3} G^{1.64/3}$$

Similarly, since the relation between area and body length, L , may be represented by the equation

$$A = 10.4L^{1.7}$$

therefore the relation of area to weight, height at withers, circumference of chest and body length is

$$A = CW^{.57/4} H^{2.4/4} G^{1.64/4} L^{1.7/4}$$

In the same manner we may include any number of measurements in our formula relating area to size of animals.

As a matter of fact, however, as shown in Figs. 4a and 4b, increasing the number of linear measurements in the formula does not increase the agreement between observed and computed values to a corresponding degree. This substantiates the idea that in the vast majority of cases the simple equation (2) involving weight only as a datum on the right

side of the equation, suffices to represent the relation between surface area and body size in domestic animals.

Properties of the power function (3):—Taking logarithms of (2) we obtain

$$\log A = \log C + n \log W \quad (10)$$

indicating that such a function gives a straight line on a logarithmic grid having slope n .

Differentiating (10), we obtain

$$\frac{dA}{A} = n \frac{dW}{W} \quad (11)$$

indicating that the percentage change in A is n times the percentage change in W . Solving for n , we obtain

$$n = \frac{dA/A}{dW/W} \quad (12)$$

indicating that the ratio between the two percentage changes is n , the exponent in the power function (2).

A numerical example will render the above ideas concrete. Let the power function be

$$A = W^2 \quad (13)$$

and let the value of the fixed multiple for successive values of W be 2; then we obtain the following pairs of values:

$$\frac{W}{A} \quad \frac{1}{1} \quad \frac{2}{4} \quad \frac{4}{16} \quad \frac{8}{64} \quad \frac{16}{256}$$

The ratio of the multiple in the A series to the multiple in the W series is seen to be

$$\frac{4}{2} = 2 = n.$$

Doubling the successive values of W quadruples the successive values of A . Increasing W according to a geometrical progression, increases A according to a geometrical progression.

This may be put in other words as follows: changing the successive values in the W series by m ($= 2$) changes the values in the A series by m^n ($= 2^2$). This shows that increasing the values in the exponent, n , according to an arithmetical progression increases the values of the multiple in the A series according to a geometrical progression. In other words, the relation between the exponent, n , of the power function, and the ratio between successive values of the dependent variable (e. g., area), when the ratio between the successive values of the dependent variable (e. g., weight), is 2, may be computed with the aid of an exponential equation, as e. g.,

$$R = e^{.693n} \quad (14)$$

in which R is the said ratio, e is the base of natural logarithms, .693 is the natural logarithm of 2, and n is the exponent in the power function. Equation (14) may be plotted on an arithlog grid as shown in Chart A enabling one to read the values of the ratio, R , for the dependent variable when the value of the exponent is known and when the ratio for successive values of W is 2.

When, as in equation (13), the power is 2, i. e., greater than 1, Y increases with increasing rapidity, and when W increases 2 times, A increases

$$e^{.693 \times 2} = 4 \text{ times}$$

When $n = 1$, then when W increases 2 times, A increases

$$e^{.693 \times 1} = 2 \text{ times}$$

that is, A increases at the same percentage rate as W ; and the power equation becomes a linear equation.

When n is less than 1 (as when area is related to weight), A increases with decreasing rapidity. Thus when $n = .70$, when then W is increased 2 times, A increases $e^{.693 \times .70} = 1.62$ times; i. e. when W increases by 100 per cent, A increases by 62 per cent. When $n = \frac{2}{3}$, then when W is increased 2 times, A is increased $e^{.693 \times .67} = 1.59$ times; i. e., when weight is increased by 100 per cent, area is increased by 59 per cent. Similarly, when $n = .56$ (as in the exponent in the equation relating area to weight in dairy cattle), increasing W by 100 per cent increases Y by $e^{.693 \times .76} = 1.47$, or by 47 per cent. Chart A will enable one to read the values directly without the necessity of computation.

Since according to equation (11)

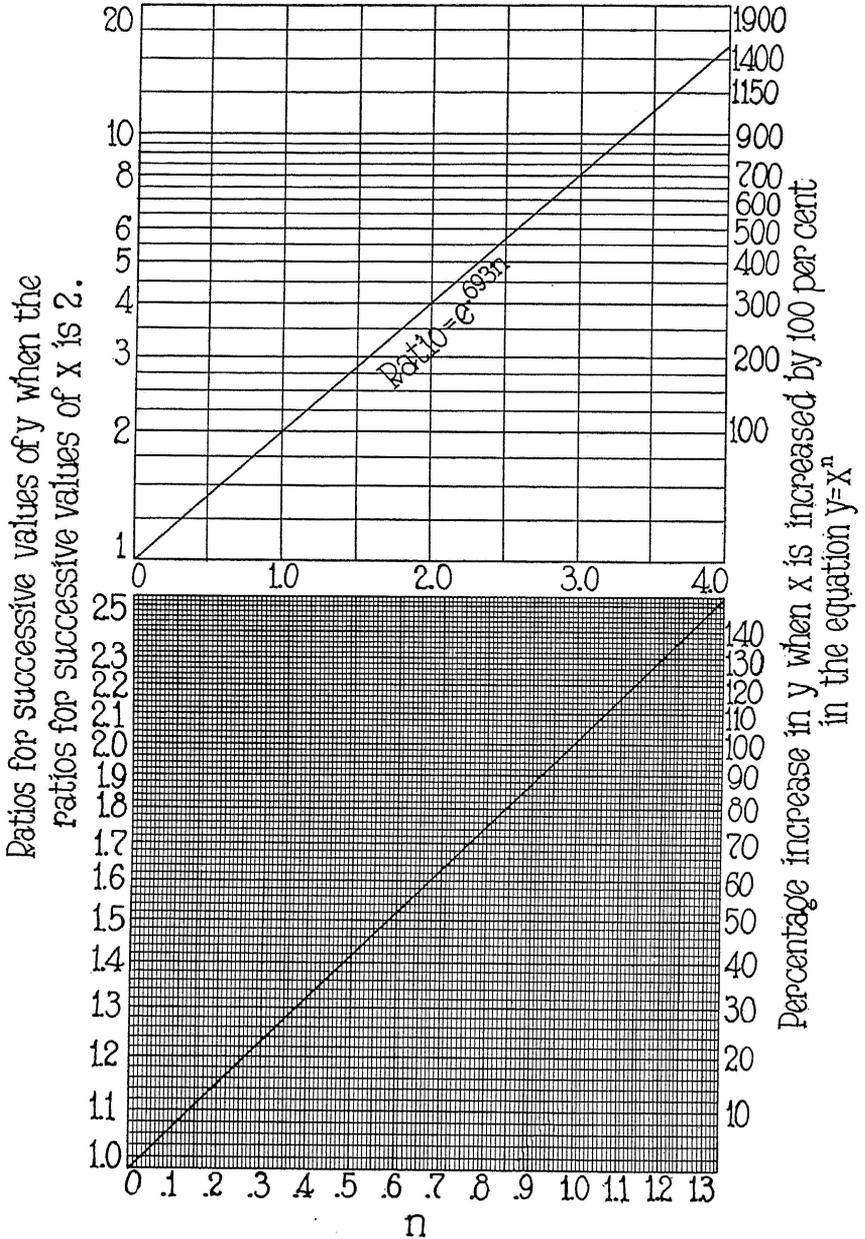


Chart A.—The relation between the change in the dependent variable (A) when the independent variable (W) is increased by 100 per cent for different values of the exponent n in the power equation $A = W^n$. Knowing the value of the exponent n in the power function $Y = X^n$, one can read from this chart the percentage increase in Y when the value of X is doubled. Thus when $n = 0.4$, then increasing the value of X by 100 per cent (i. e. doubling it), increases the value of Y by a little over 32 per cent. See text for further explanations.

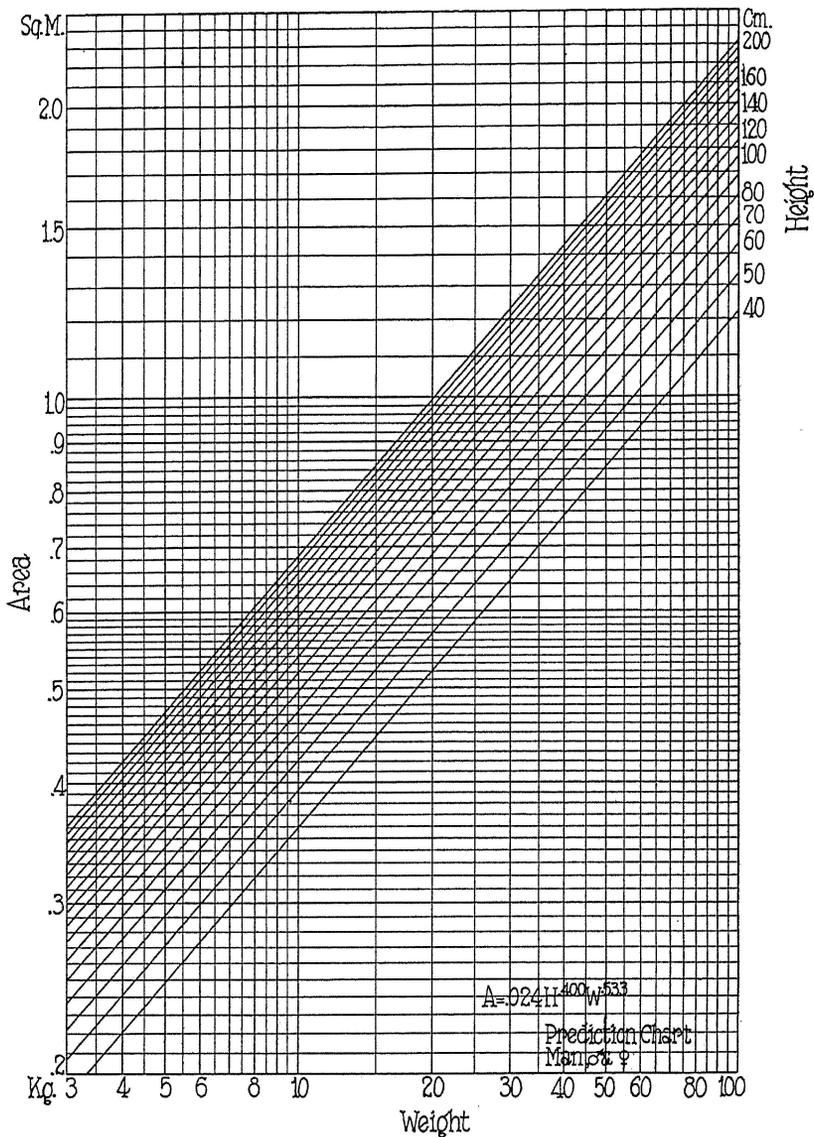


Fig. 5.—A chart for estimating area (based on the formula given on the chart) when weight and height are known. (Note: when weight only is known, the areas may be estimated from Fig. 1, or from Fig. 2.) The agreement between the area as estimated from this chart and the true area, can not be greater than the agreement between the average curve and the observed data as indicated in Fig. 1. In other words, the difference between predicted and true areas may be as great as 10 per cent. According to our conception the percentage of error may be still greater when using the formula of Du Bois as indicated in Fig. 1, the second curve from the bottom.

$$\frac{dA}{A} = n \frac{dW}{W} \quad (11)$$

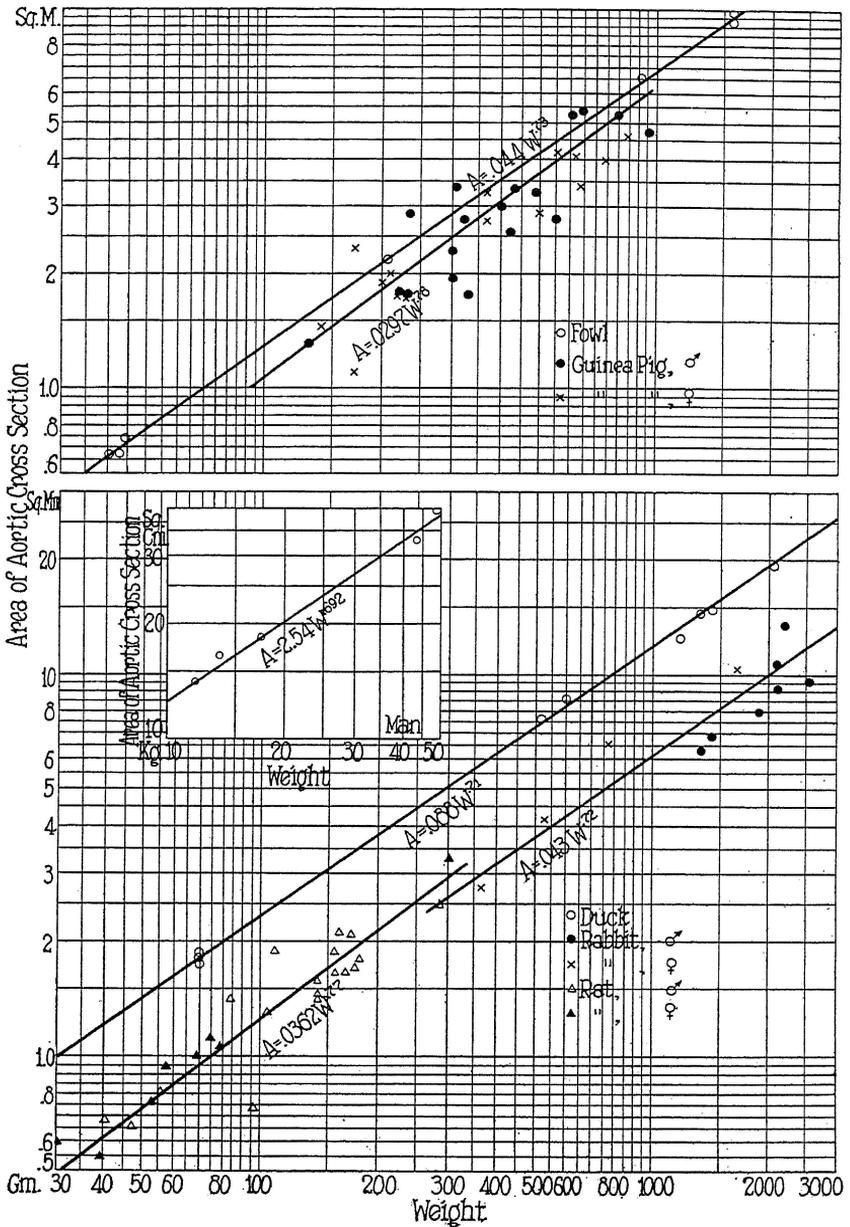
the percentage change in A equals the percentage change in W times the value of the exponent n , the question might be raised why not simply multiply the percentage change in W (weight) by the exponent, n , in order to obtain the percentage change on A (area), i. e., why not simply say that the percentage change in A is n times the percentage change in W . The answer to this question is that equation (11) is concerned with limiting values; it contains the terms dW and dA which represent *very* small (i. e. limiting) changes in W and in A , too small for their use in practical problems. It can not be used for relatively large percentage changes (because the slope of the power function is not constant). When, however, it is possible by some mathematical device to translate our question into the form of an *exponential* equation, as we have done in the case of equation (14), then it becomes possible to find the relation between percentage changes of A and W (area and weight) no matter how large the percentage changes. This possibility arises from the fact that, as in equation (14), we are comparing percentages i. e., logarithms, in a function which plots as a straight line on a logarithmic (i. e., relative, which is equivalent to a percentage) scale, so that the percentage change at any point is *always* proportional to the value of the ordinate at that point; and when the base e is used, it is equivalent to the value of the ordinate for the given percentage change. This, by the way, explains in part at least the wide use of natural logarithms when dealing with relative rates (the rate of increase of the exponential function, $Y = e^{kx}$, at any point is always proportional to the value of the function at that point.)

The preceding analysis of the properties of equation (2), makes it clear that it is easy to prepare a prediction chart based on equation (9) including height and weight. When height remains constant, then equation (9) is reduced to the same form as equation (2), and therefore when area is plotted against weight on an arithlog grid a straight line should result of slope .53, and intercept $240H^{.40}$ (or $.024H^{.40}$ when dealing in square meters). Fig. 5 shows such a weight-height-area prediction chart for man.

II. THE SIGNIFICANCE OF SURFACE AREA IN ENERGY METABOLISM

During the course of the present investigation questions have come up concerning the theoretical interest and the practical utility of this work on surface area. This section is presented in order to save similar misgivings in others who may undertake to reinvestigate the relation between surface area and body size. The polemic between Benedict and Lusk, Du Bois and their followers is well known. For this reason it will not be considered here.

Before reviewing the situation as we see it, it may be useful to recall the fact that the degree of proportionality between heat production and area (or weight) may be determined by plotting heat production against body weight on a logarithmic grid, then determining the slope of the curve. If the slope is 1, then heat production is directly proportional to weight; if the slope is of the order of $\frac{2}{3}$ (similar to the slope relating area to weight) then heat production is directly proportional to area. Employing this simple procedure for testing the degree of proportionality between surface area and heat production we obtain the following facts:



Figs. 7a to 7e.—The area of the aortic cross section, the area of the tracheal cross section, blood volume, and vital capacity all appear to increase with increasing body weight at approximately the same relative rate as does surface area. Plotted data by Dreyer and co-workers.

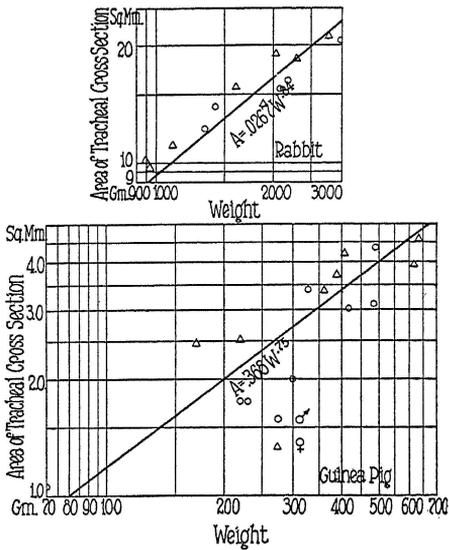


Fig. 7b.

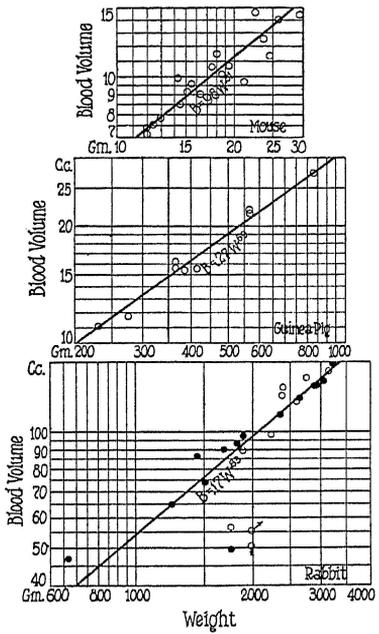


Fig. 7c.

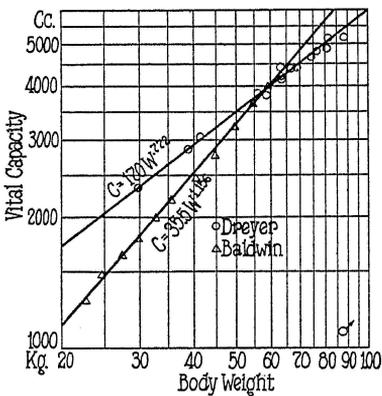


Fig. 7d.

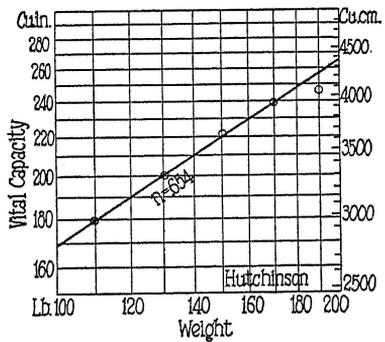


Fig. 7e.

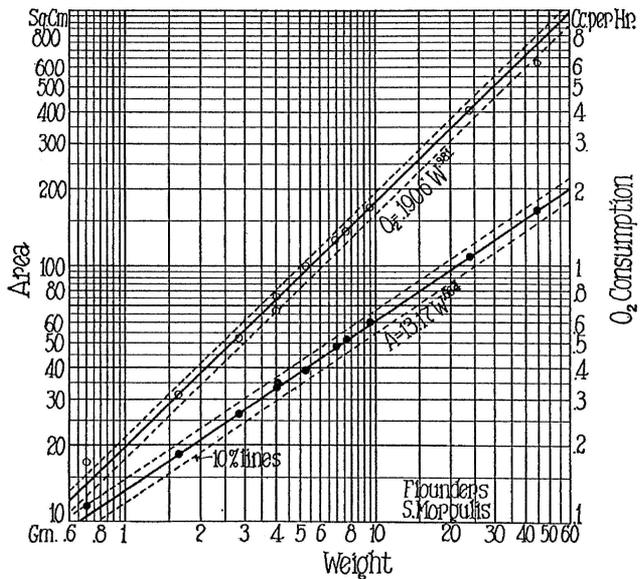


Fig. 8.—While the area (A) of the flounder increases directly with the .66 power of its weight, the oxygen consumption (O_2), and therefore its heat production, increases directly with the .98 power of its weight; that is, heat production is, practically, directly proportional to body weight.

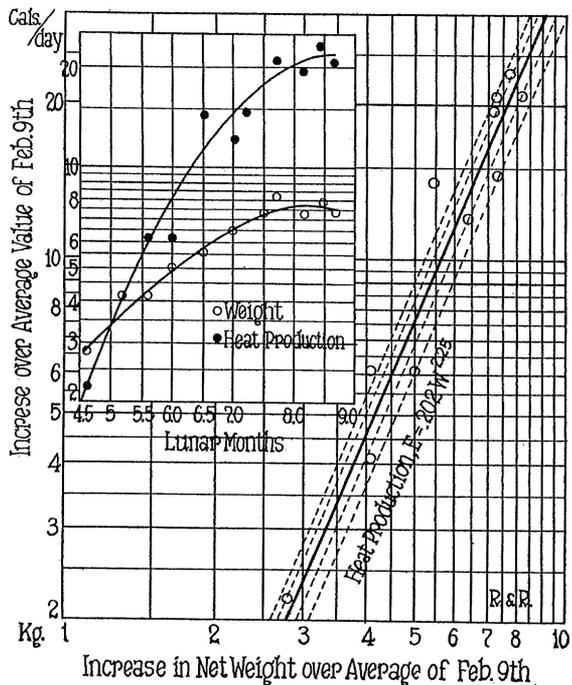


Fig. 9.—The relation between increase in heat production and increase in body weight in a woman during gestation. It appears that the increase in relative heat production is over twice as great as the increase in relative body weight. Surface cannot therefore be considered as a controlling factor in heat production during pregnancy. (Computed and plotted from data by Root and Root, Arch. Int. Med., 1923, XXXII, 414).

increase with body-weight at approximately the same relative rate as does surface area. This has been pointed out before by a different technique by Dreyer and co-workers.

3. Fig. 8 indicates that in the flounder, heat production is (practically) directly proportional to body weight and not to surface area.

4. Fig. 9 indicates that during pregnancy, heat production increases even more rapidly than body weight.

5. Fig. 10 shows that during fasting, heat production decreases

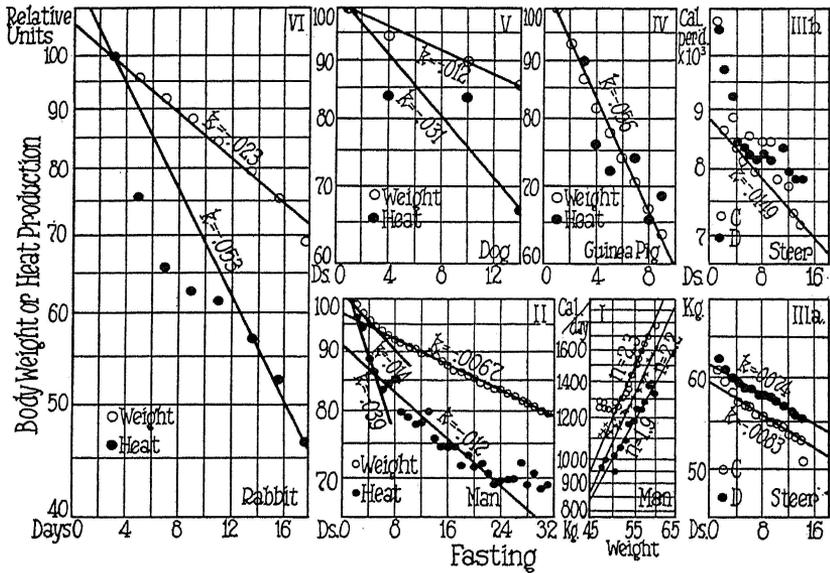
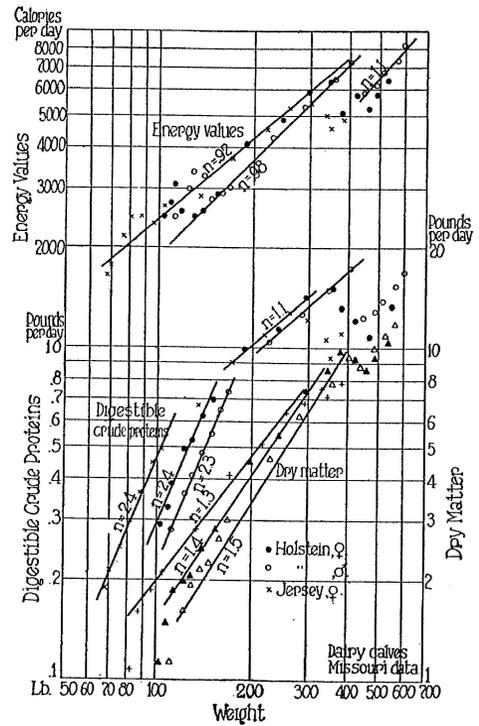
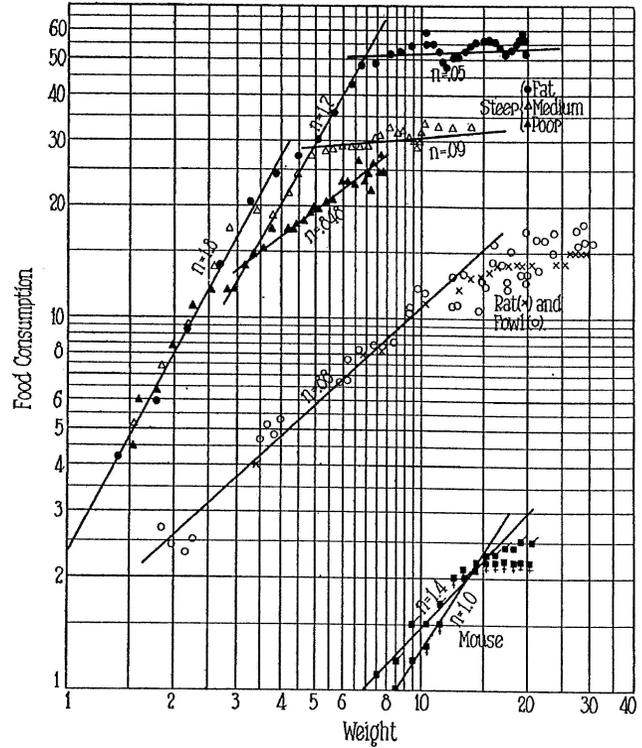


Fig. 10.—The relative decline in body weight and in heat production during fasting. Chart I represents heat production plotted against weight on logarithmic coordinate paper (data by Benedict on Levanzin, as given in Publication 203, Carnegie Institution of Washington). The values of the exponent, n , in the power function (roughly, 1.9 for heat production when asleep, 2.2 heat production on awakening in the morning, 2.3 total heat production) indicate that the percentage change in heat production is about twice as great as the percentage change in body weight. In II the same data are plotted on an arithlog grid. The ratio of the slopes, k , gives roughly the same value as the value of the exponent ($\frac{.012}{.0067} = 1.8$) in I. IIIa and IIIb present a similar comparison for steers C and D during fasting (see Benedict and Ritzman Carnegie Publication 377, pp. 166 and 168, April 18 to May 1, fast). The ratio of the slopes is roughly 2 ($= \frac{.0149}{.0078}$); that is, the percentage decline in heat production is about twice as great as the percentage decline in body weight. IIIb represents heat production plotted against days fasting IIIa represents body weight plotted against days of fasting. Similar comparisons are made for the rabbit (VI), and dog (V), and guinea pig (IV). In the dog and the rabbit the percentage decline in heat production is, roughly, double that for the percentage decline in weight. In the guinea pig, the percentage decline in heat production is the same as the percentage decline in body weight. IV, V, and VI represent data by Rubner as cited by Voit (Z. Biol. 1901, XLI, 113). It is certain that the decline in heat production during fasting, and presumably the increase in heat production during re-alimentation (it is curious that while so much has been done on fasting, no such attention has been given to the process of re-alimentation), does not vary directly with body surface.



Figs. 11a and 11b.—The relation between body weight and food consumption during growth. The curves for dairy calves are based on unpublished data. The other curves are based on data as follows: Steers by Moulton, Trowbridge, and Haigh; Fowl by Jull; Rat by Wang; Mouse by Thompson and Mendel. The values of the exponents, n , fluctuate around 1; i. e., the increase of body appears to be directly proportional to the food consumption, or the food consumption appears to be directly proportional to the body weight, at least up to a certain age.

On the chart containing the curves for such widely differing animals as mouse, steer, and fowl, the position of the decimal point on the axis varies of course with the size of the animal. Thus 20 grams in the mouse corresponds to 200 grams in the rat, 2000 grams in the fowl and 200 kilograms in the steer.

more rapidly than body weight (during re-alimentation the heat production presumably increases more rapidly than body weight).

6. Figs. 11a and 11b indicate that food consumption during growth tends to increase directly with body weight (or body weight tends to increase directly with food consumption).

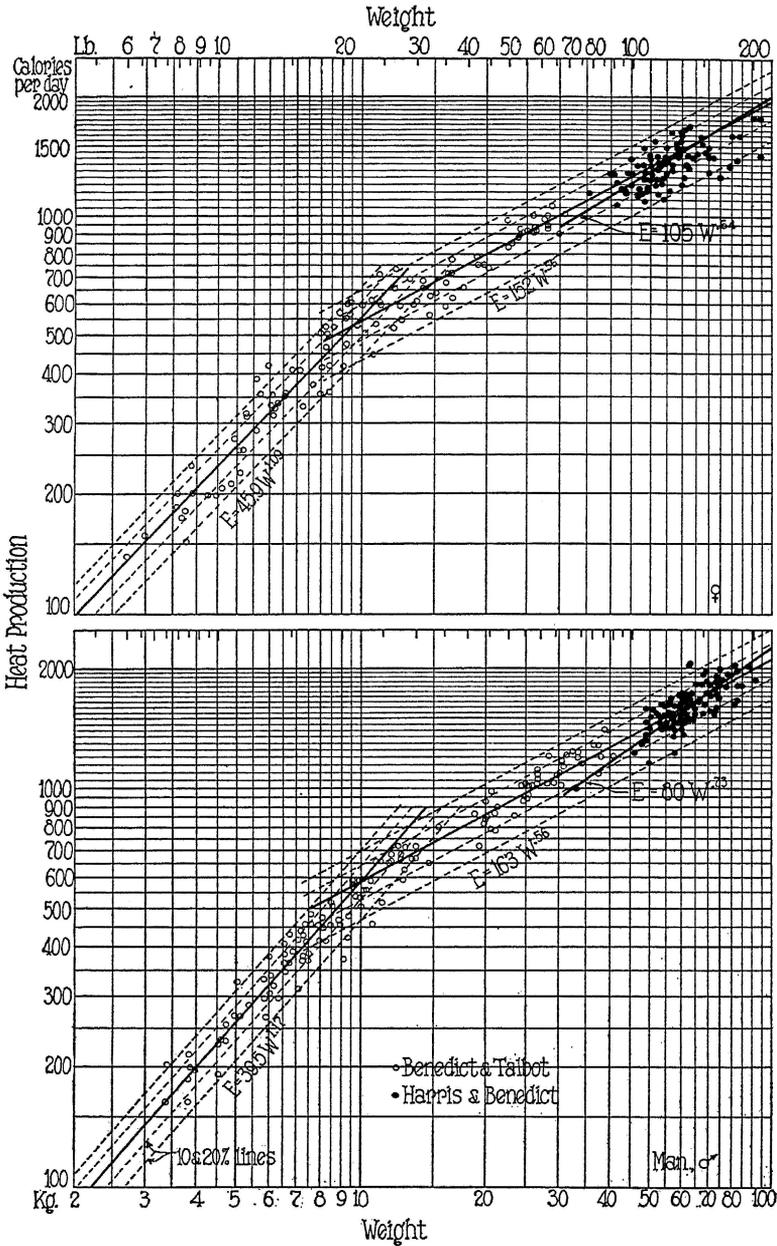
7. Figs. 12a and 12b show that during the first year, heat production in children increases directly with body weight or even somewhat more rapidly than body weight. Following the age of one year, heat production increases variously from the .56 to the .73 power of body weight, while we have found that surface area increases directly with the .68 power of body weight.

8. Finally, we do not quite see the logic involved first in relating area to body weight (thus introducing one set of errors); then computing area from body weight (thus introducing a second set of errors); and finally, relating heat production to the computed area. Why not relate heat production to body weight directly in the first place with the aid of equation (2), or simply with the aid of charts such as are given in Fig. 12?

We do not quite see how the statement "heat production varies directly with body surface" is any better than the statement "heat production varies directly with the .56 or with the .67 power of body weight". Any one who understands the meaning of the power function (2), as explained in the preceding section, understands one of these statements as well as the other.

It must be granted, however, that since it is customary to express heat production per unit area, this expression gives a feeling of definiteness and concreteness which is rather lacking in a mere formula when one does not understand it.

The central thought of the present discussion is that there is no *necessity* for bringing area into the problem of heat production when one measures not area but weight, or weight and height. If one desires a "norm" or standard for basal metabolism then why not use a chart, such as Fig. 12, or the uppermost curve in Fig. 1, or Figs. 39, 40, 41, and 42?



Figs. 12a and 12b.—The relation of heat production to body weight. Note that, following the age of one year, the value of the exponent varies from .56 to .73. Preceding one year, heat production increases directly with body weight. This direct proportionality between heat production and body weight preceding one year is substantiated by Fig. 12b., page 25, in which heat production is plotted against body weight for infants of the same age (new-born infants).

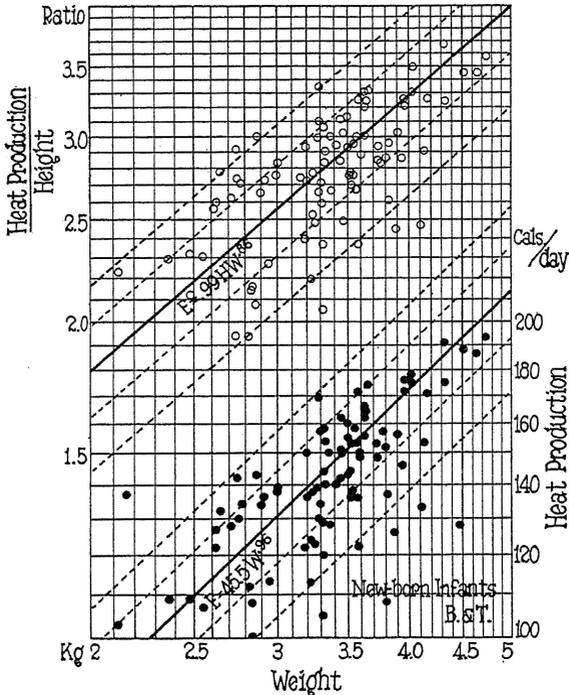


Fig. 12b.—The relation of heat production to body weight (lower curve) and to the product of height and weight (upper curve) of newborn infants. Data by Benedict and Talbot.

III. THE NEW DATA ON SURFACE AREA

Regardless of our opinion concerning the significance of surface area in metabolism, we have conscientiously investigated the new data on surface area (which, as pointed out, includes 482 dairy cattle, 431 beef cattle, 12 horses, 12 swine). We have also examined the data on 47 young women measured at this Station by Mrs. Bradfield (Missouri Agr. Exp. Sta. Research Bulletin 109).

Fig. 13 includes all (341) measurements on beef cattle, including all ages, and all degrees of fleshiness. The equation is given on the chart. The slope is seen to be .56 (not .67). All data points are within 10 per cent of the average curve.

It should be noted that in the case of dairy cattle, carefully measured under the very best conditions, the data points fall within 5 per cent of the average as shown in Fig. 14. The data on beef cattle were obtained under extremely unfavorable conditions. The animals were wild, not used to being handled, very excited, and annoyed by flies in the hottest part of the summer. The large number of data points were obtained in

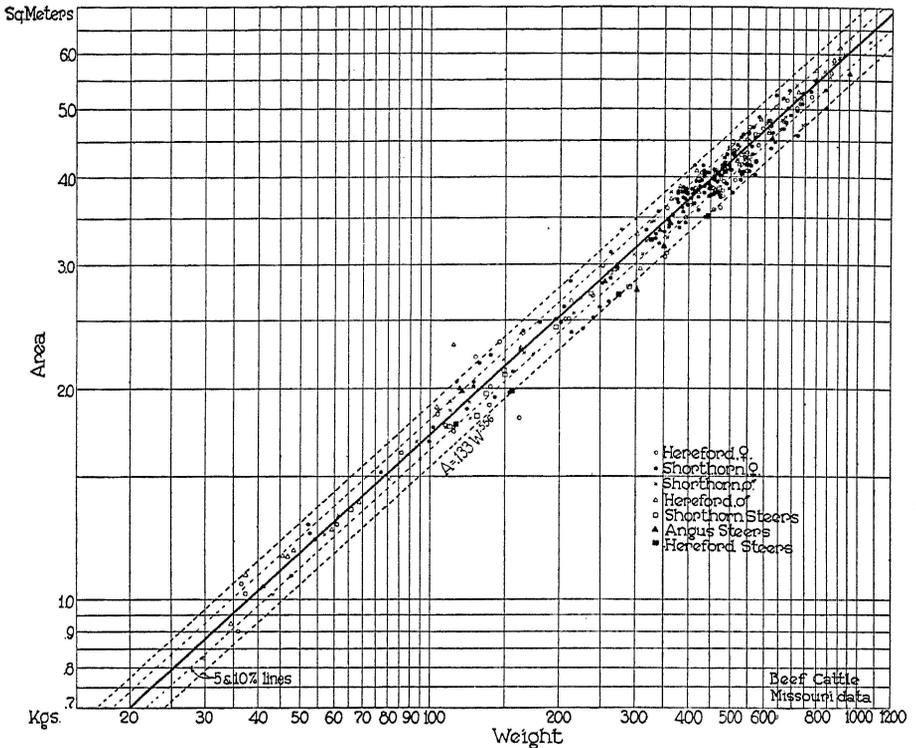


Fig. 13.—The relation between surface area and body weight in beef cattle, including both sexes and all states of nutrition. This chart represents 341 animals.

order to compensate for the errors in the measurements due to the unfavorable conditions under which the measurements were made.

Additional charts for beef cattle, divided according to breed, sex, etc., are given in the appendix.

Fig. 15a presents all the new data on dairy cattle (measured by Mr. Matthews). The data published in Res. Bul. 89 (measurements by Elting) were also included in this chart. The difference in slope between these two sets of data consists in the fact that Elting measured the area of the tail, while Matthews did not. 15b shows the new data plotted by breeds.

Additional charts representing Matthews' measurements are given in Figs. 13 and 14, Res. Bul. 96 of this series, and in the appendix of the present bulletin.

The new data on horses are included in Fig. 16; the new data on swine are included in Fig. 17.

Including a linear datum in the formula relating area to body size did not improve the degree of agreement between observed and computed values.

It may be noted incidentally that since in cattle, area is directly proportional to (roughly) the square of height at withers, therefore (as explained in section I) when height at withers is included as a datum in the formula relating area to body size, the proper value of the exponent for height is 1 ($m = 1$). In the appendix several charts are shown in which the ratios of area to height are plotted against the corresponding weights. The agreement between observed and computed values is no better in these charts than in the ones in which height is not included as a datum in the formula; in case of Fig. 16, it is much worse.

The poorer agreement between observed and computed values in the charts based on Matthews' measurements (Fig. 15) than in the chart based

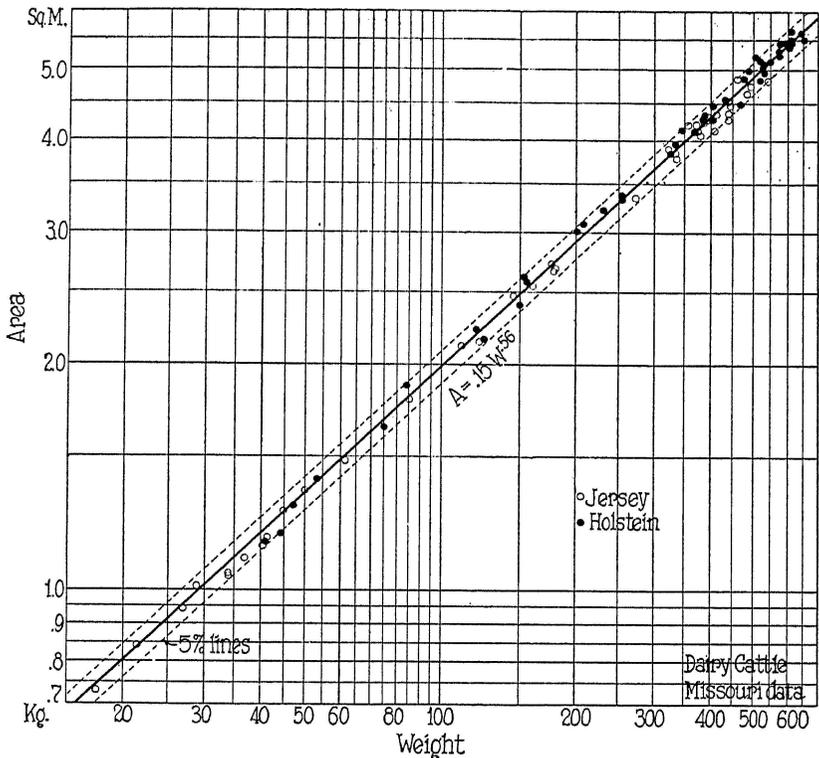


Fig. 14.—Cattle when carefully measured with the surface integrator under ideal conditions do not deviate by more than 5 per cent from the average curve, even if all ages and two breeds are included as is the case with the animals on this chart. This chart is the same as Fig. 4 in Res. Bul. 89, but with the 5% lines drawn in so as to show the percentage deviations from the average.

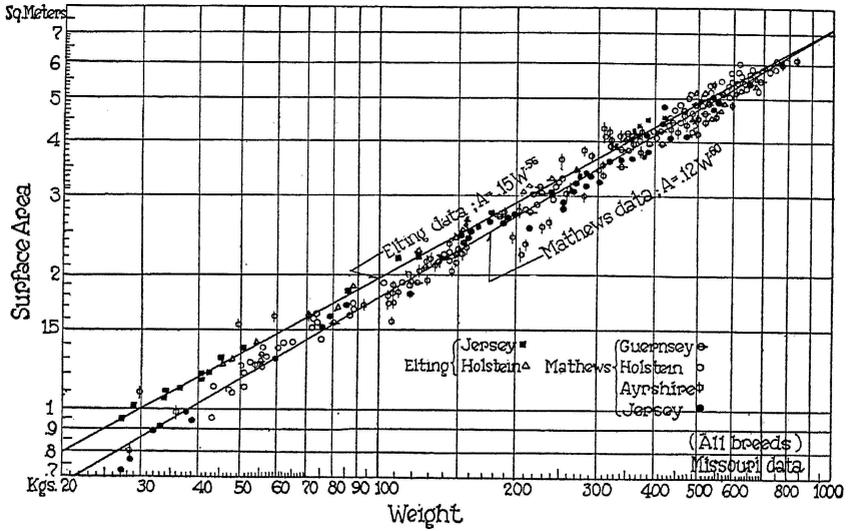


Fig. 15a—The relation between area and weight of the new data (482 animals) on dairy cattle. For further explanations see text.

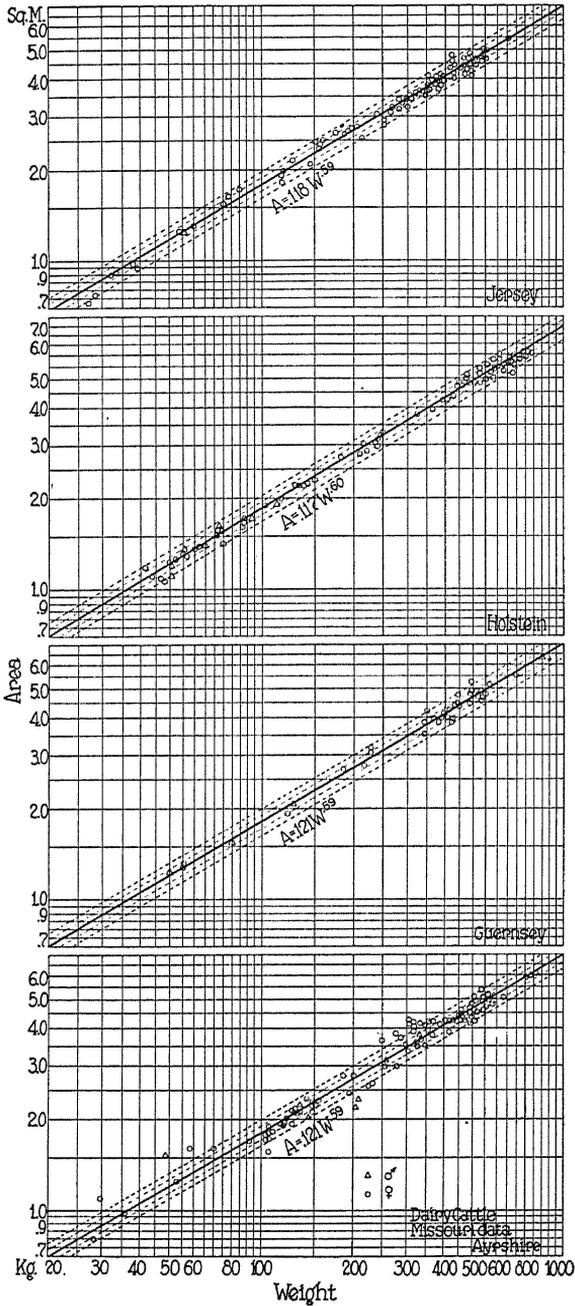


Fig. 15b.—The relation between surface area and body weight in the several breeds of cattle. Breed differences with respect to this relationship are insignificant.

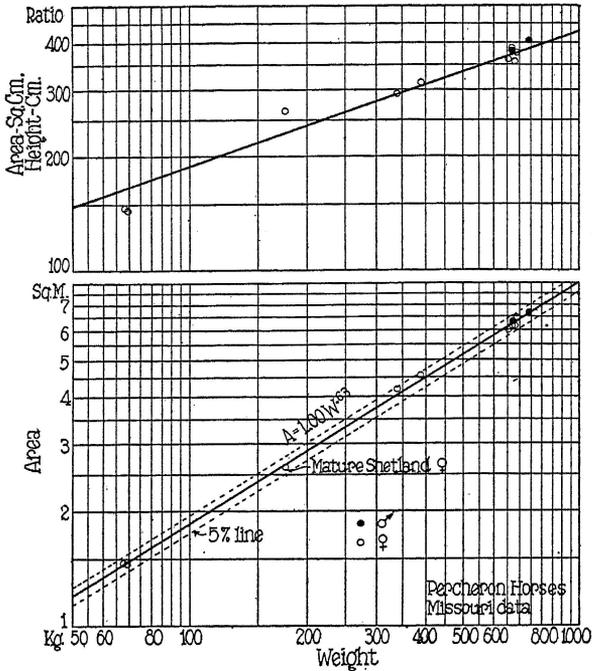


Fig. 16.—The relation between surface area and body weight of horses. Including a linear datum in the formula increases the deviations between the observed and computed values.

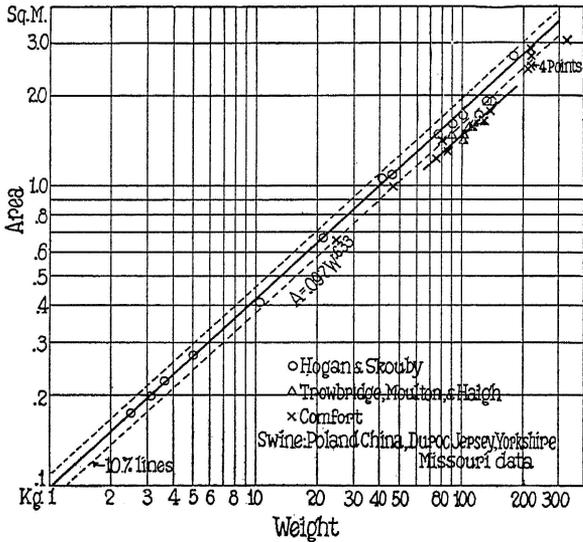


Fig. 17.—The relation between area and body weight of swine. The crosses which represent the new data are 10 per cent below the averages of Hogan and Skouby.

on Elting's measurements (Fig. 14) is explained by the fact that while Elting confined his measurements to animals belonging to the University of Missouri herd, Matthews measured animals belonging to several other herds. It was difficult to measure many of these animals, because, unlike college herds, they were not used to being handled.

Hannah Stillman Bradfield of the Home Economics Department of this Station employed the surface integrator for measuring the surface

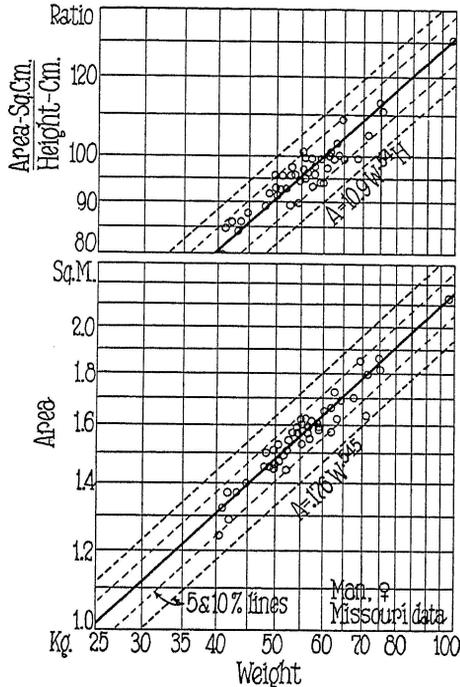


Fig. 18a.—The relation between surface area and body weight of the subjects measured by Mrs. Bradfield. The upper curve includes height ($m = 1$) as a datum. Note that the value of the exponent is .55 and not .68 as indicated in Fig. 1. Note also that the data points (49 individuals), including the very heavy individual, are distributed within the 5% limits. Note also that the exponent of weight did not change by including height, H , as a datum in the formula.

area of young women (of approximately college age). She measured 47 individuals. Details of her work together with the numerical data are given in a dissertation (University of Missouri Library, 1927) and in Research Bulletin 109 of this Station (1928). We have plotted her data with the result shown in Fig. 18a. The value of the exponent of equation (2) for these data is only .55 as compared to .68 found in Fig. 1. This low

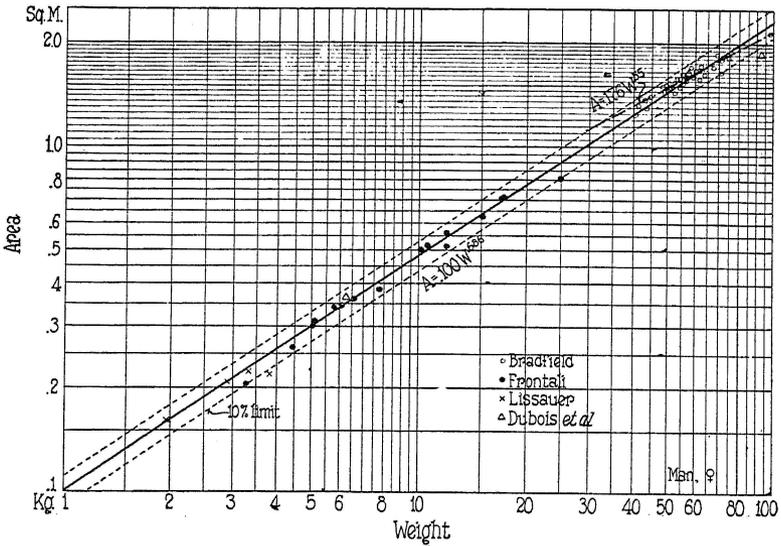


Fig. 18b.—The relative distribution of Mrs. Bradfield's data when plotted on a chart of wide range so as to include all weights and ages. This chart shows that the slope of the line relating area to weight is less for mature individuals (height nearly constant) than for growing individuals (weight as well as height increase). The triangle on the extreme right represents Mrs. McK. Note that an individual heavier than Mrs. McK., measured by Mrs. Bradfield, falls on the average line.

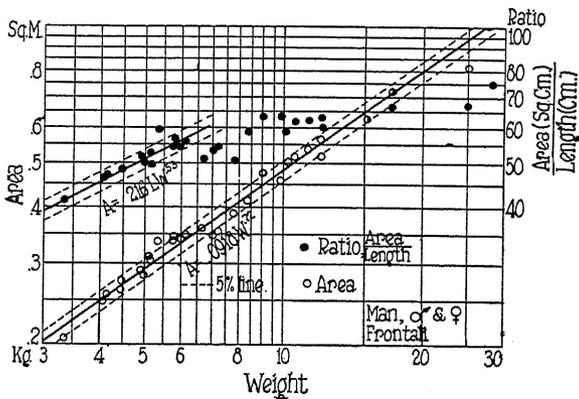


Fig. 18c.—The relation between surface area, A, and body weight, W, and the relation between area, weight and height, L, in man. Plotted from data by Frontali.

value of the exponent is also indicated in Fig. 18b in which Mrs. Bradfield's measurements were plotted together with other measurements including very young children.

The low values of the exponent for Mrs. Bradfield's data are due

to the fact that as compared to the range in weight, the range in height for these individuals is relatively very low. It has already been explained that when one wishes to combine an equation relating area to weight

$$A = C_1 W^n \tag{a}$$

with an equation relating area to height

$$A = C_2 H^m \tag{b}$$

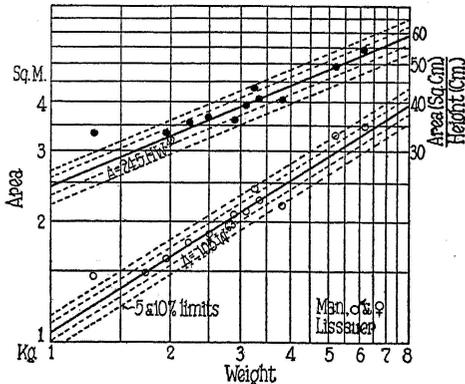


Fig. 18d.—The relation of area to body weight, W, and to height, H. Plotted from data by Lissauer.

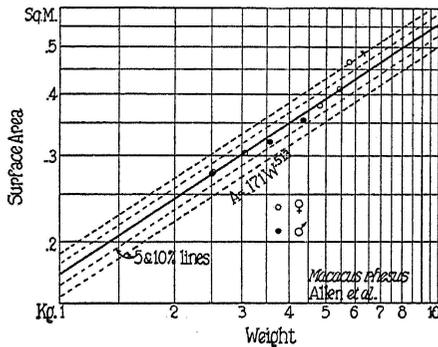


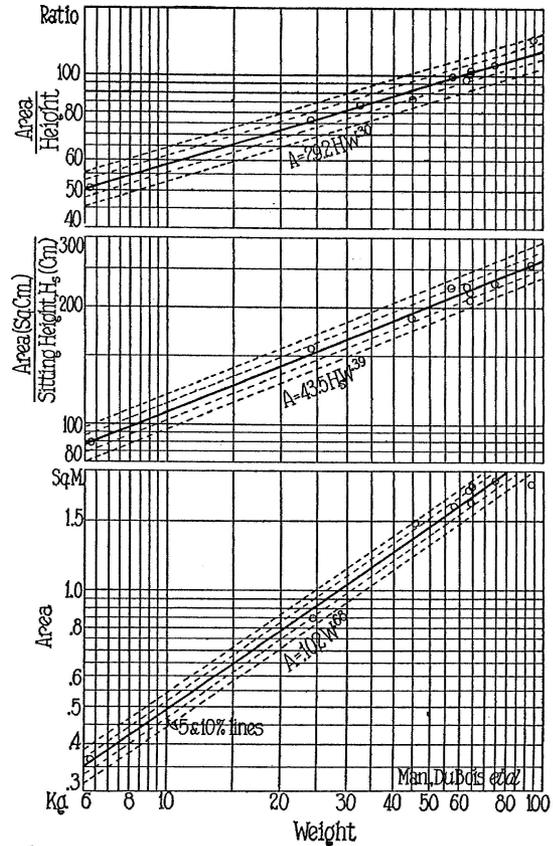
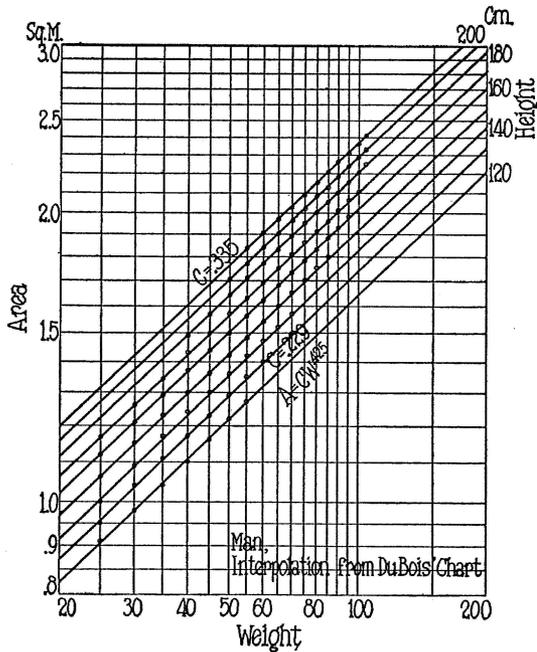
Fig. 19.—The chart relating area to weight in monkeys may be of interest in this connection. These data were obtained with the surface integrator in Dr. Edgar Allen's Laboratory of the University. Dr. Allen may publish the numerical data and a chart based on them elsewhere.

then in the combined equation the values of the exponents are halved

$$A = C H^{m/2} W^{n/2} \tag{c}$$

But when the height remains roughly constant, as in the case of Mrs. Bradfield's subjects, then H^m in (b) above is roughly constant, and consequently CH^m is roughly constant so equation (c) becomes

$$A = C_4 W^n$$



Figs. 20a and 20b.—The relation of area to weight, W , to sitting height, H_s . ($=$ Height $- (O + R)$); and to height, H . Note that area is proportional to weight raised to the power .68; when height is included as a datum in the equation, the area is proportional to weight raised to the power .30. The chart on the right shows that the slope of the curves for constant heights, as interpolated from the Du Bois prediction chart, is .425. See text for further explanations.

In other words, in equation (1) when height as well as weight changes (as during active growth), the value of the exponent n is greater than when weight increases and height remains nearly constant. When the height remains absolutely constant while weight increases, the value of n in equation (c) would be the same as in equation (a); when weight remains constant and height increases, then the value of m would be the same in (c) and in (b); when both change as during active growth, the values of m and n in (c) are approximately half of the values in (a) and (b).

As a further illustration of the influence of the relative constancy of height on the value of the exponent of weight we may plot the areas for various weights, but for constant heights, on a logarithmic grid, using for this purpose data interpolated from the Du Bois prediction chart. The slope, n , of the lines is seen in Fig. 20a to be .425 (the value of the exponent for weight as given by the Du Bois formula). But when height is not included as a datum, then the value of the exponent is not .425, but .68 as shown in Fig. 20b.

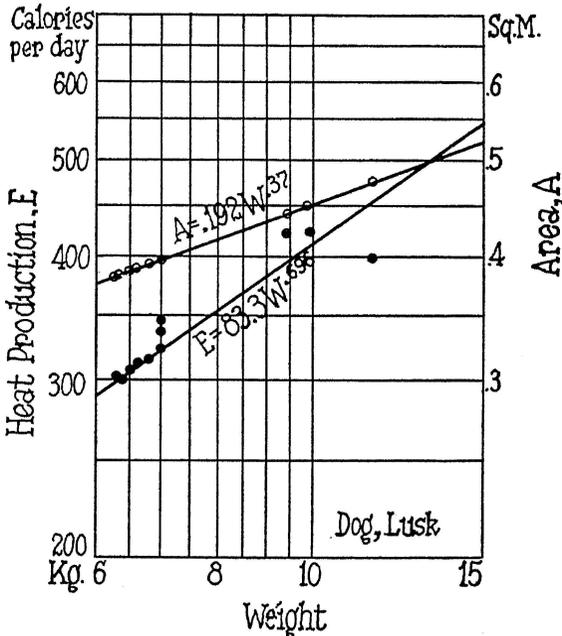


Fig. 21.—A comparison of the increase in heat production, and the increase in surface area with increasing body weight of dogs XIX and XXVII in Lusk's Laboratory. Plotted from data cited by Cowgill and Drabkin. Compare with Fig. 34b.

We may conclude, therefore, that in animals of approximately the same height, the area varies not with the $\frac{2}{3}$ power of weight, but with some smaller power of weight.

It may be permissible to point out what appears to the writer as a fallacy. Fig. 21 represents the increase in heat production with increasing weight of two adult dogs of the same body length (Dogs XIX and XXVII in Lusk's Laboratory). The heat production is seen to increase directly with the .70 power of the weight, while the surface area (as computed by Cowgill and Drabkin, page 47) increases with the .37 power of the body weight. There appears to be, therefore, an error in assuming that heat production is directly proportional to surface area. If Fig. 21 represents the situation correctly, then heat production increases almost 1.9 times as rapidly with increasing weight as does surface area. The fallacy, if present, consisted in assuming that surface area in animals of *constant length* increases directly with the $\frac{2}{3}$ power of the weight. (Figure 21 is an illustration favoring the inclusion of the height datum in the formula relating to body size).

One practical conclusion from this discussion is that investigations having for their aim the quantitative evaluation of heat production per unit surface of an *individual* can not rely on a formula derived from data on a *population*. Individual variability does not permit the application of averages to individual cases. This statement should be evident to a biologist or even to the layman. It is the discrepancy between average expectations and individual variations which forms the basis of such an eminently practical business as life insurance.

In quantitative investigations between heat production and body surface, the individual animal must be measured. The surface integrator described in Research Bulletin 89 of this Station offers a practical method for measuring the area directly. Quite recently, after the appearance of the aforementioned Research Bulletin 89, Frontali published a photograph of an integrator apparently designed many years ago by Bordier. Frontali's instrument, together with his table of data, is reproduced in Fig. 22.

SUMMARY AND CONCLUSIONS

In addition to the presentation of the data and the charts as outlined in the abstract, this work may be summarized as follows:

1. The surface area is directly proportional to some power of the body weight. Meeh assumed the value of the power to be $\frac{2}{3}$. As a matter of fact, the value of this power varies, in *our experience*, from about .32 to .72 depending on the form of the animal. The change in form of the animal due to increase in weight during growth is quite different from the change in form of mature animals during fattening or fasting. The lowest value of the power is for fattening; the highest for growth. Including a linear datum in the formula is helpful in many

cases in compensating for differences in body form in the prediction of surface area.

2. The use of a prediction chart, or a prediction formula (necessarily formulated on the basis of measurements of a population) for estimating the surface area of an individual may involve an error as high as 10 per cent of the true value.

3. Because of the necessarily large error involved in applying to an *individual* a formula based on the measurement of a *population*, it is suggested that if it is desired to relate heat production to body surface of an individual, a surface integrator should be used in actually measuring the area. It is perfectly proper however to use a formula for large-scale computations on *populations*.

4. While the practice of relating heat production to surface area may be justified by custom it is entirely unnecessary in principle. It appears that all vital organs in the body increase directly with some fractional power of the body weight, the value of this power being within the limits of the value of the power for weight, in the equation relating area to weight. (That is to say, the relative increase in mass of the various supporting and connecting tissues in the body is greater with increasing body weight than the increase in mass of the vital organs (viscera)). Incidentally, this differential nature of growth may be one—if not the chief one—of the factors limiting the size of the body. This being the case, it is no more rational to relate heat production to surface area than to the weight of the (one, or all) vital organs. It is simpler to relate heat production to a power of body weight or to powers of weight and height (especially with the aid of logarithmic paper) than to relate heat production to surface area, either by measuring surface area directly, or by using a formula which may introduce into the result an error as high as 10 per cent.

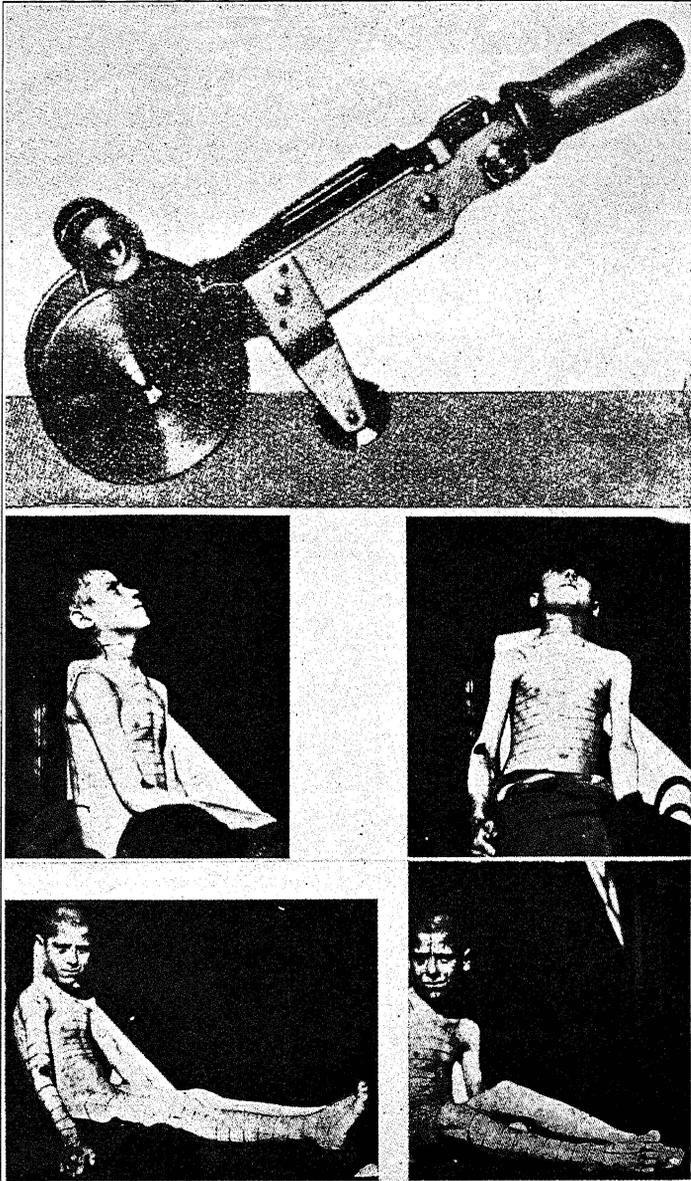


Fig. 22.—A photograph of Bordier's device for measuring area recently used by Frontali (made by Jules Richard, 25 Rue Melingue, Paris) and a photograph of a subject illustrating the method of using the integrator. Mr. Gus Thornsjo, mechanician University of Missouri, made the surface integrator described in Res. Bul. 89 of this series. The data by Frontali are on page 39.

N.º d'ordine	Sesso	NOME	Età	Statura cm.	Peso kgr.	Superficie calcolata			Superficie misurata totale	Superficie misurata per Kg.	Superficie misurata per cm. statura	Osservazioni
						Vierordt- blech (cost. 11.07)	Lissauer (cost. 10.5)	Du Bois				
1	f.	Ghironi ..	g. 24	50	3.305	2642	2273	2308	2060	624	41.2	(111 cal.p.kg.)
2	m.	Muscas ..	m. 1	53.5	4.050	3025	2603	2331	2482	612	46.4	(109 cal.p.kg.)
3	m.	Desogus ..	m. 1 1/2	54	4.130	3064	2637	2372	2541	615	47.0	
4	f.	Caredda ..	m. 2	57	5.140	3545	3050	2701	3004	584	52.7	
5	m.	Dro	m. 2 1/2	56	4.900	3434	2955	2613	2897	591	51.7	
6	m.	Piras	m. 2 2/5	57	5.305	3676	3112	2738	3378	637	59.2	sogg. pastoso
7	f.	Fenu	m. 3	54.5	4.455	3223	2773	2460	2619	588	48.0	
8	m.	Serra	m. 3	56	4.980	3471	2987	2631	2802	562	50.0	
9	f.	Maccioni ..	m. 3	58	5.105	3529	3036	2727	3100	607	53.4	
10	m.	Taglias ..	m. 4	56.5	4.450	3221	2771	2524	2732	614	48.3	
11	m.	Farris	m. 4	63	6.000	3930	3381	3102	3403	567	54.0	
12	m.	Enardo	m. 4 1/2	62	5.150	3549	3054	2873	3083	598	49.7	
13	m.	Giacobbè ..	m. 5 1/2	60	5.755	3822	3289	2941	3391	589	56.5	
14	f.	Monnis	m. 6	62	6.100	3973	3419	3088	3449	565	55.6	(100 cal.p.kg.)
15	f.	Dessi	m. 7	63	5.795	3848	3304	3056	3446	594	54.6	
16	m.	Cabriolu ..	m. 10	65	7.000	4354	3747	3388	3461	494	53.2	(91 cal. p. kg.)
17	m.	Asuni	m. 10	64.5	7.200	4437	3818	3409	3505	486	54.3	
18	f.	Putzu	m. 11	70.5	6.660	4187	3625	3518	3613	542	51.1	(90 cal. p. kg.)
19	m.	Ullu	m. 12	70	8.325	4798	4206	3675	4119	494	58.8	(88 cal. p. kg.)
20	m.	Pisano	m. 15	72.5	9.830	5459	4697	4225	4597	467	63.4	
21	m.	Ambu	m. 20	74.5	9.000	5148	4429	4161	4728	525	63.4	
22	f.	Genotini ..	m. 23	85	10.200	5595	4814	4829	5004	490	58.8	
23	m.	Sechi	m. 24	85.3	11.300	5990	5154	5057	5313	470	62.2	
24	f.	Porcedda ..	m. 24	86	12.060	6256	5384	5241	5164	428	60.0	
25	f.	Sanna	m. 29	76.6	7.800	4680	4027	3986	3856	494	50.3	sogg. ipotrof.
26	f.	Cardia	m. 30	83.5	10.650	5759	4955	4856	5172	485	61.9	
27	f.	Zara	a. 4	90	12.050	6252	5379	5453	5623	466	62.4	
28	m.	Sanna	a. 4	85.7	12.050	6252	5379	5262	5179	429	60.4	
29	f.	Porcu	a. 5 1/2	98.6	15.200	7299	6280	6371	6250	411	63.3	
30	f.	Fanni	a. 7	100.5	17.075	7884	6785	6786	7118	416	70.8	
31	f.	Porcedda ..	a. 8 1/2	108	17.200	7924	6818	7174	7157	416	66.2	
32	m.	Meloni	a. 9 1/2	134	28.200	11013	9478	10347	10052	355	74.7	
33	f.	Carta	a. 12	121.5	25.600	10404	8953	9158	8075	323	66.4	

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APPENDIX

The charts giving the relation between area, weight, and linear size of the original data that could not be incorporated conveniently in the body of the text are given in the appendix.

The original data on surface area as measured with the surface integrator having been analysed, it appeared desirable to analyze in similar manner published data on surface area. This we did. The resulting charts are presented in this appendix. In this way this bulletin becomes a fairly complete summary of the available data on surface area.

Since the interest in the surface area problem is a development of the suggestion that heat production is proportional to surface area, it seemed natural to want to examine the heat production data in the same manner as we have examined the data on surface area. Accordingly several charts on the relation between heat production and body weight have also been prepared, and the results are presented in this appendix.

We have not attempted to list values for heat production per unit area as computed by the new formulae, as the reader can easily compute such values for the particular set of data in which he is interested. All that he will need to do is to read from the chart (or compute from the given formula) the area for the desired weight, then take a similar reading for heat production for the desired weight, and divide the value for heat production by the value for surface area for the given weight.

An alternative method, illustrated by the following example on the dog, suggests itself. From Fig. 36, heat production is related to weight (in the dog) by the evaluation

$$E = 88.6W^{.66} = C_1W^n$$

When weight is one kilogram, $E = 88.6$ calories. From Fig. 34b, area is related to weight (in the dog) by the equation

$$A = .10W^{.696} = C_2W^m$$

in which A is area in sq. meters, and W is weight in kilograms. When weight is one kilogram, $A = .10$ sq. meters, and heat production per sq. meter is therefore $88.6 \times 10 = 886$ calories. In other words, heat production per unit area = $\frac{C_1}{C_2}$.

Since this procedure involves extrapolation to one kilogram, and since in many cases the law relating area to weight, or heat production to weight, is not known for weight one kilogram, therefore this method must be used with caution. There is, of course, no objection against using this method if one considers the theoretical heat production for weight one kilogram as an empirical constant in the same sense that one considers, for instance, the Meeh constant as empirical.

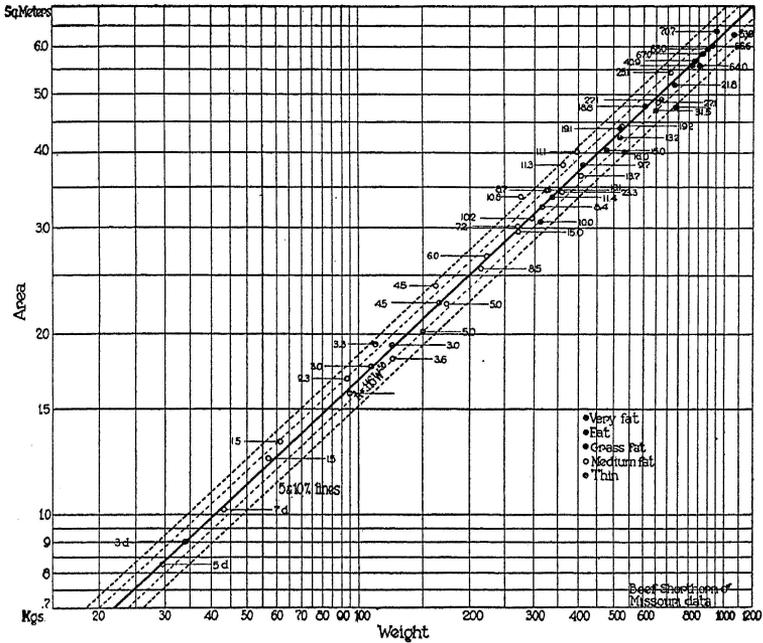


Fig. 25a.—Shorthorn males.

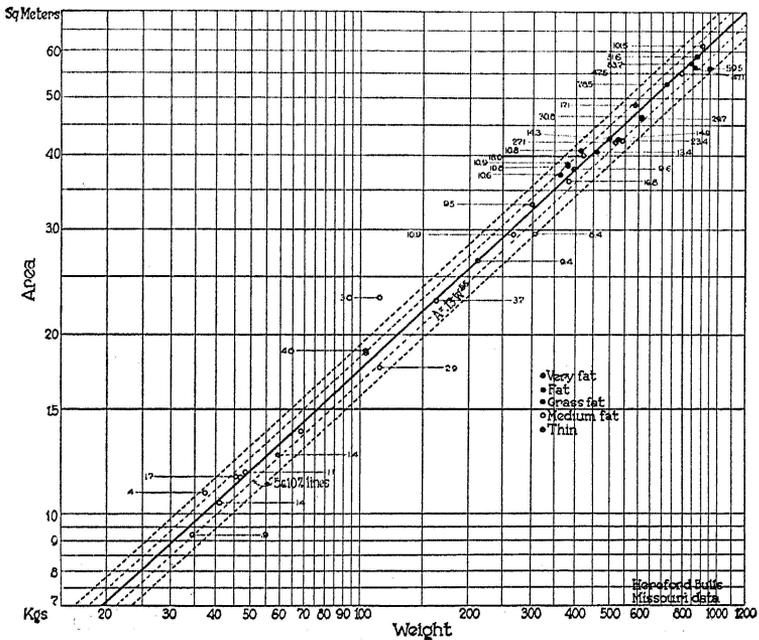


Fig. 25b.—Hereford males.

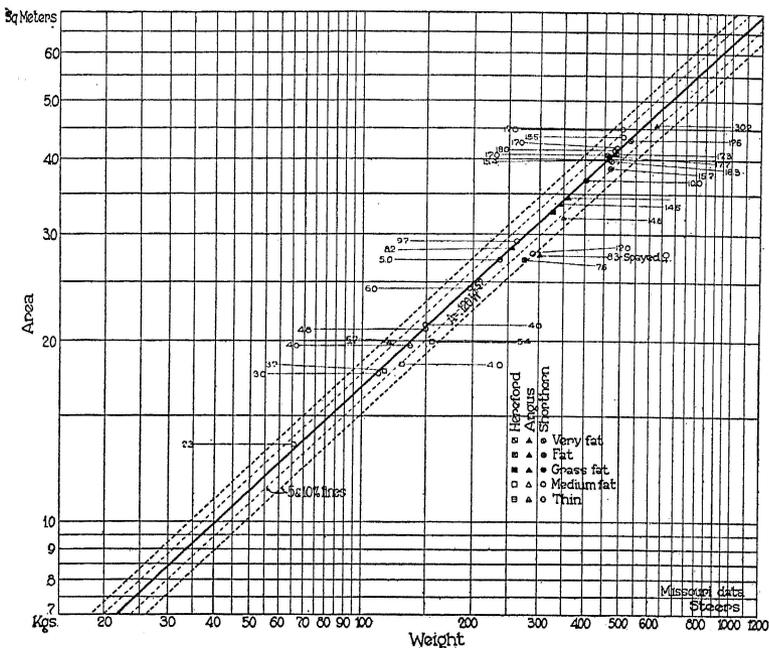


Fig. 26.—Steers.

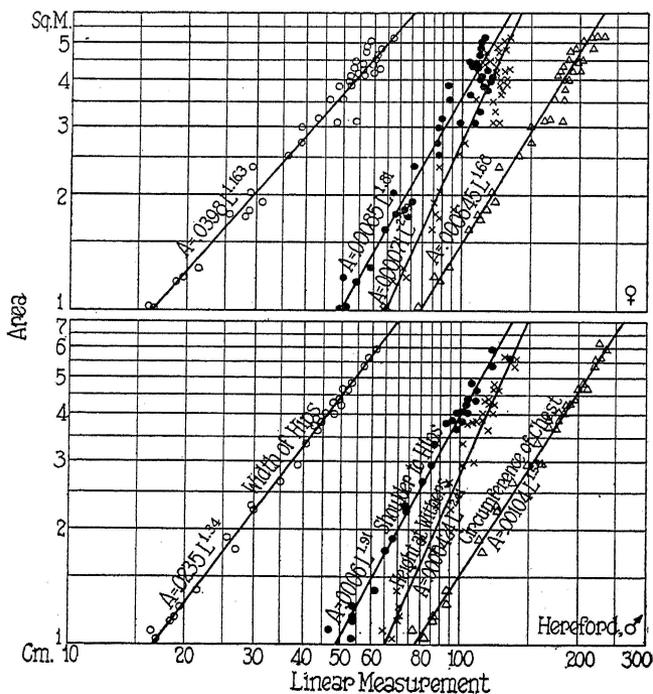


Fig. 27.—The relation between area and several of the linear measurements for Hereford cattle. These results are typical of all breeds of beef cattle, so the results for the other breeds are omitted.

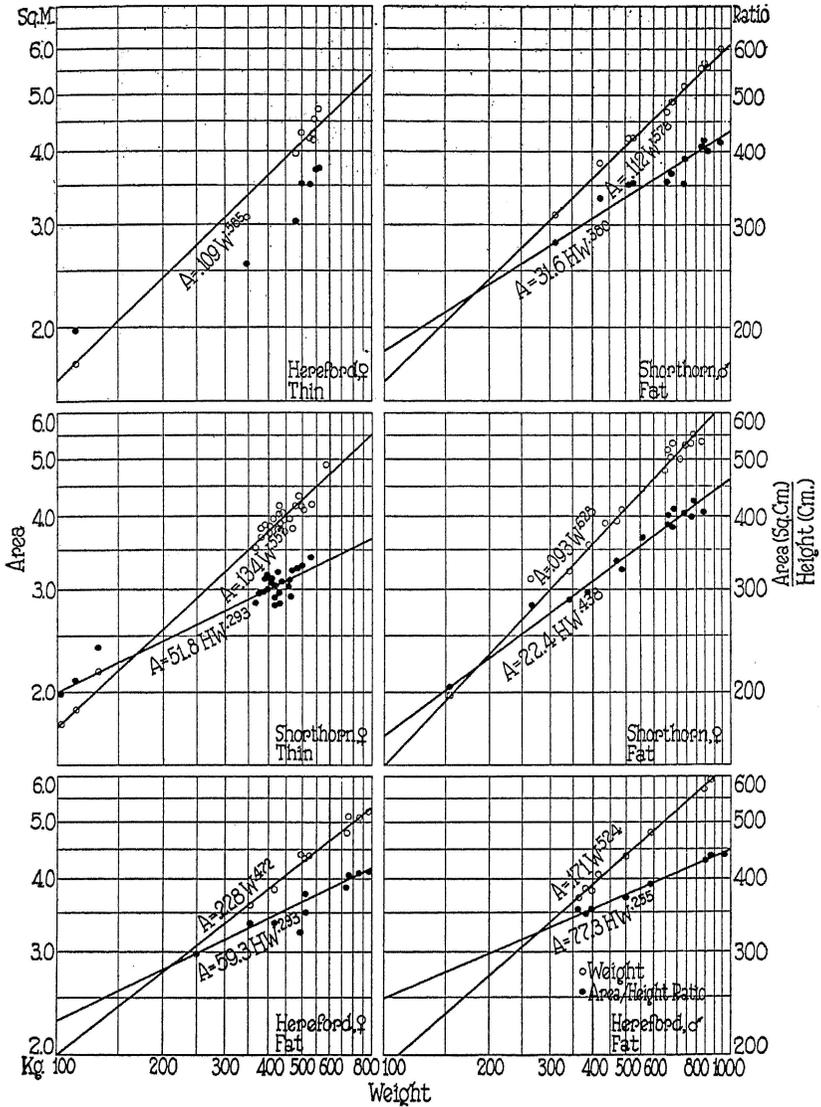


Fig. 28.—An attempt has been made to determine the influence of the degree of fatness on the slope of the curves for the beef cattle. The animals were accordingly separated into "thins" and "fats" and their areas were plotted against weight as shown; the ratios of the areas to the heights were also plotted. In interpreting the curves, it should be remembered that the data represent growing animals; that is, the comparison is made between young fat (or thin) animals and mature fat (or thin) animals. This is an altogether different matter from comparing the areas of animals of the same age (and therefore of the same linear size) during fasting or fattening. The latter problem was suggested to us for investigation by Dr. E. B. Forbes, Director of the Institute of Animal Nutrition at State College, Pa. We planned to carry it out. However, the expense involved in such an undertaking together with the results of the present investigation, which make it difficult for us to see the significance of the problem, caused us to hesitate in undertaking it. The results of this chart are not consistent. In some cases the exponents are higher for fat animals (Shorthorn, females), while in others the exponents are higher for the thin animals (Hereford females). Open circles represent the relation of area, A, to weight, W, and to height at withers, H. Full circles represent the relation of area, A, to weight, W, and to height at withers, H.

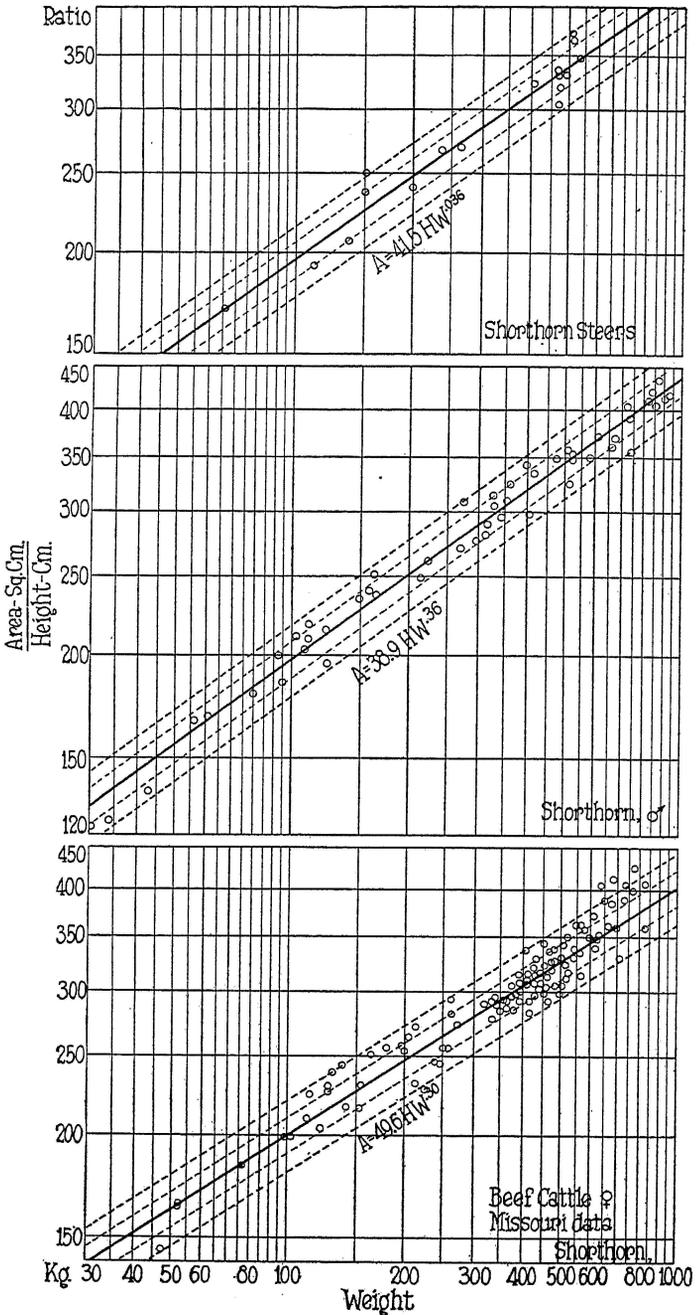


Fig. 29a.—The relation area, A, to weight, W, and to height at withers, H.

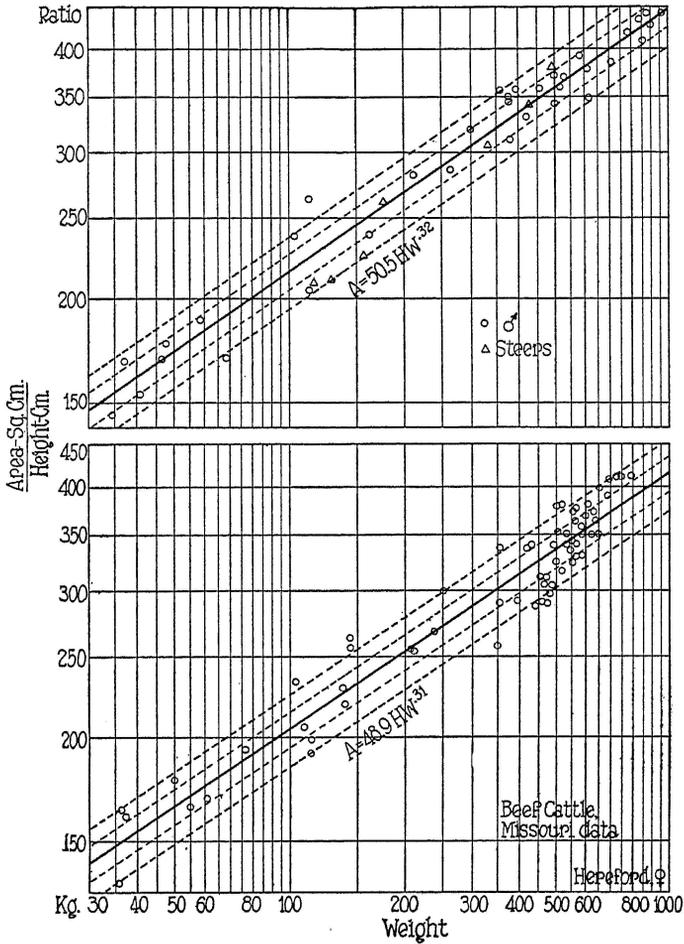


Fig. 29b.—The relation of area to weight and to height in beef cattle. The broken lines represent 5 and 10 per cent deviations from the average.

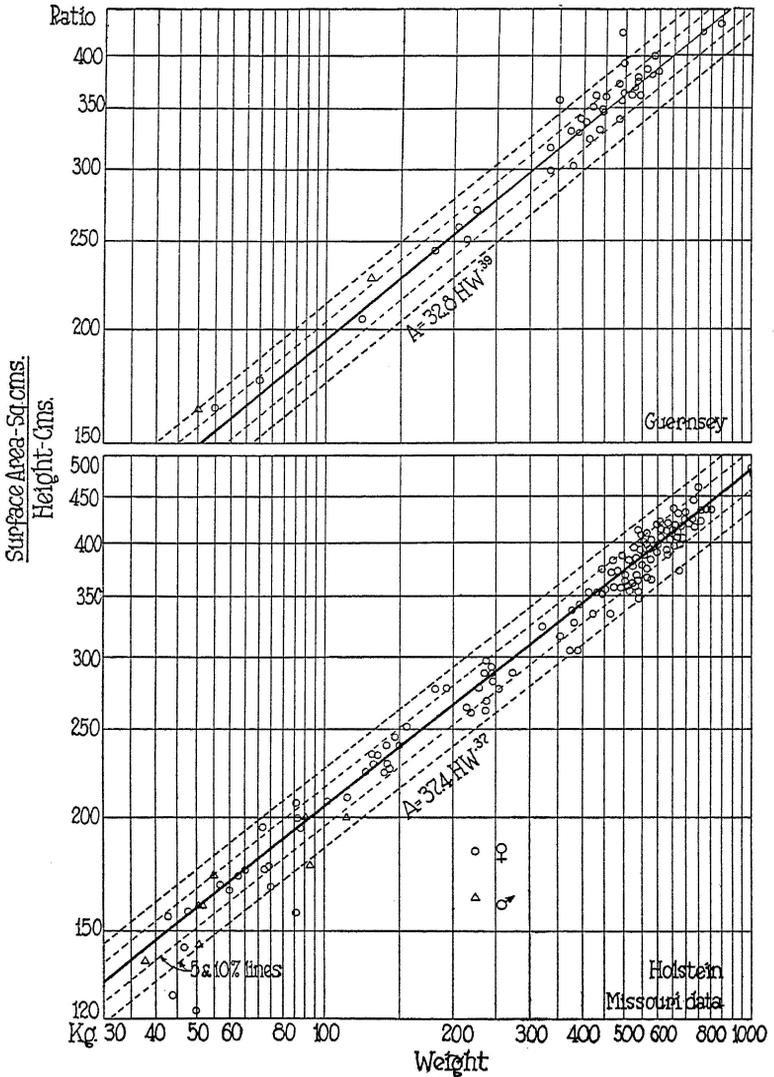


Fig. 30.—The relation of area to weight and to height of dairy cattle.

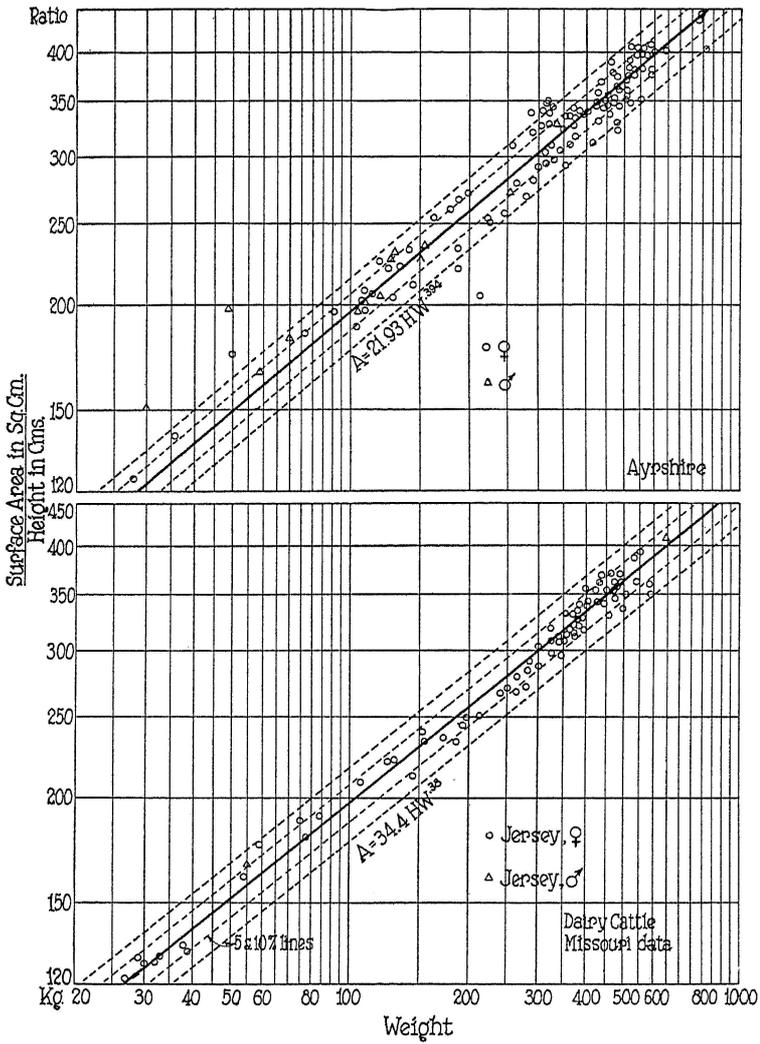


Fig. 31.—(Continued).

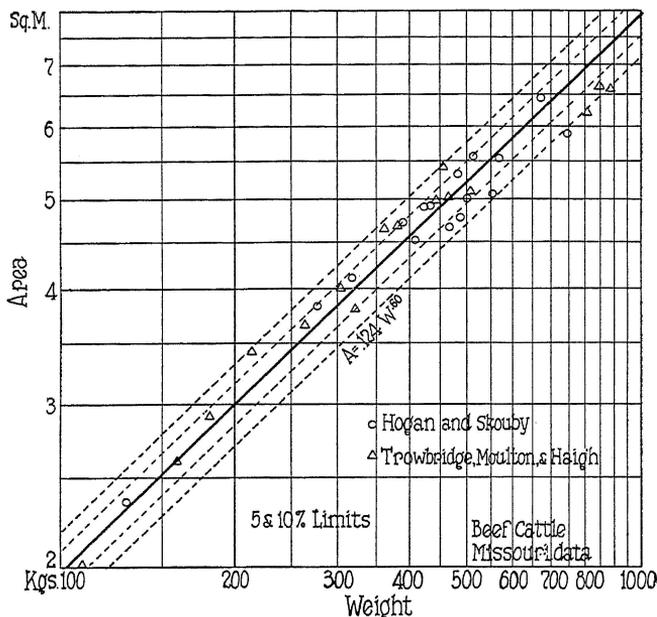


Fig. 32.—The relation between area and weight plotted from data by the investigators indicated on the chart. The chart includes all the animals measured, the fat as well as the thin animals. Hogan and Skouby measured the area by the mold method of DuBois. Trowbridge *et al.* skinned the animals and measured the hide directly. The formula proposed by Hogan and Skouby: $A = 217.02 W^{.4} L^{.6}$. The formula proposed by Moulton: For fat animals, $A = .158 W^{.556}$; for other animals, $A = .1186 W^{.625}$.

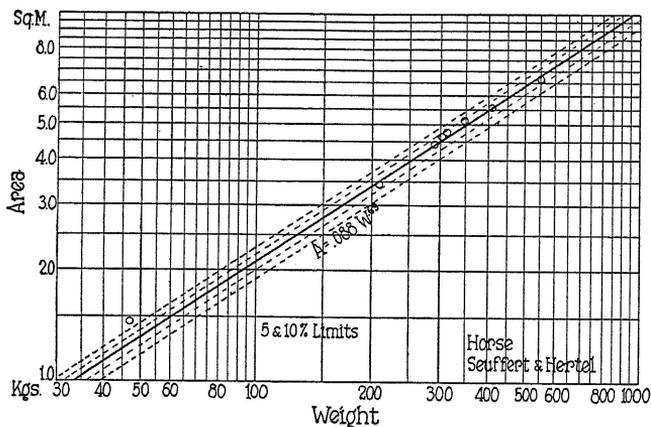
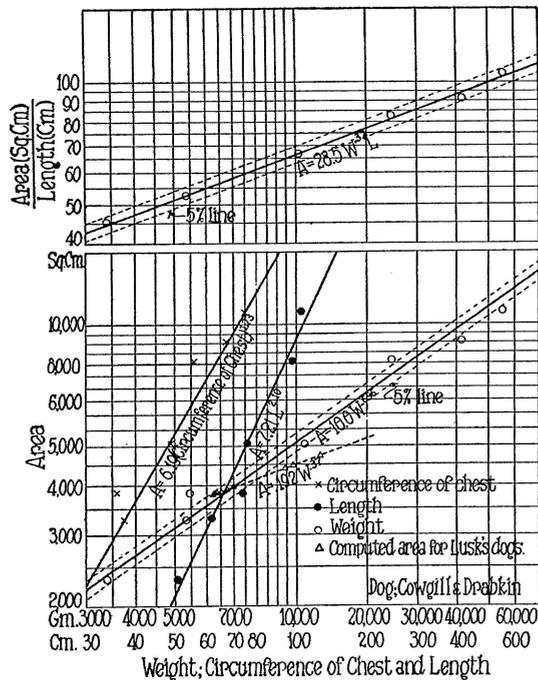
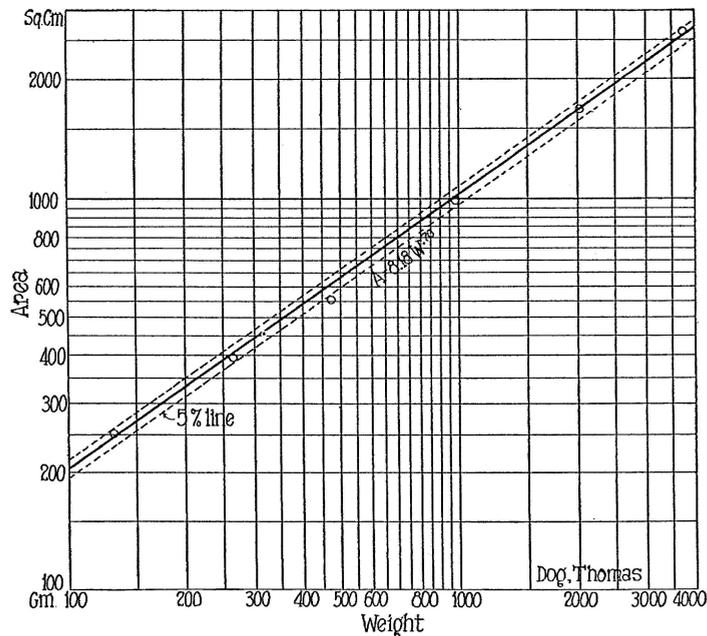


Fig. 33.—The relation between area and weight plotted from data by Seuffert and Hertel. The animals were skinned, the skin was photographed with a given reduction, and the area was computed from the weights of the prints. Compare with Fig. 16, and note the difference in (1) slope and (2) coefficient (i. e., area for a given weight.)



Figs. 34a and 34b.—The relation between area, A , and weight, W , in the dog. The upper half of Fig. 34b on the right based on the data by Cowgill and Drabkin indicates that in the case of animals of different weight but of the same body length the area indirectly is proportional to weight raised to the power .37. This is substantiated by the curves passing through the triangles in the lower half of the figure. The later curve represents dogs XIX and XVII in Lusk's Laboratory (quoted by Cowgill and Drabkin) both of which have approximately the same body length. When, however, both length and weight vary, the area is proportional to the .70 power of the weight. The conclusion is

that the exponent in the equation relating area to weight is different for growing animals, or for animals of different body weight but in the same state of nutrition, than for animals of the same linear size but in different states of nutrition. Compare with Fig. 21.

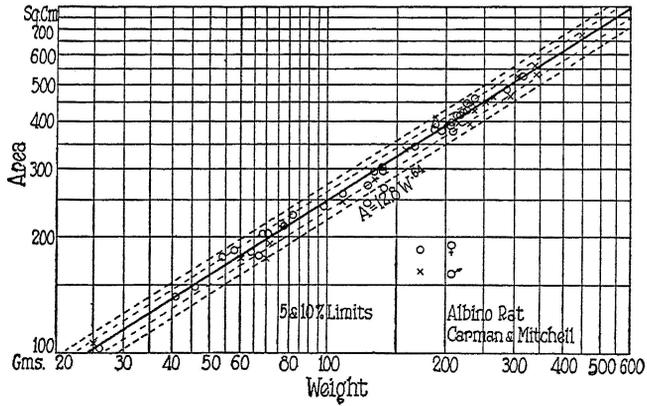


Fig. 35.—The relation between area and weight in the rat.

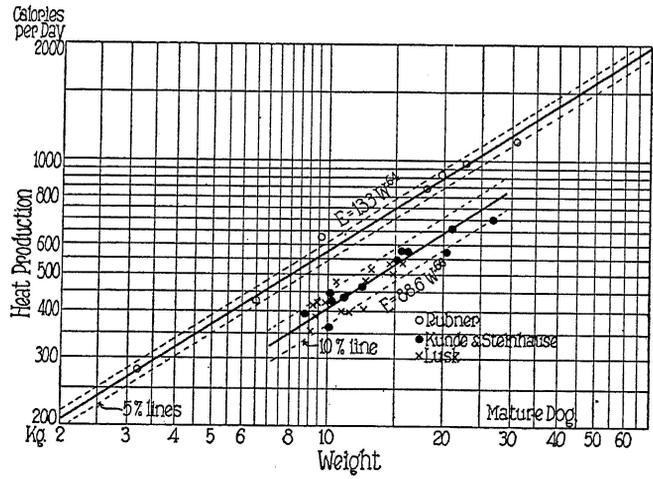


Fig. 36.—The relation between heat production and body weight in the dog. This figure shows that heat production is directly proportioned to weight raised to the power .65. Fig. 34 shows that in dogs varying in linear size as well as in weight (i. e. in dogs of the same body form) the area is directly proportional to weight raised to the power .70; in animals of the same body length but of different weight (i. e., differing in body form), the area is proportional to weight raised to the power .37. The answer to the question whether heat production is or is not proportional to surface area therefore depends on how the area varied with weight of the animals represented in this chart. From Lusk's data (see Fig. 21) it appears that heat production tends to be proportional to the $\frac{2}{3}$ power of weight even if area varies only with the .37 power of weight. The upper curve represents the measurements by Rubner (1883, p. 542); the lower curve represents the measurements by Lusk and by Kunde and Steinhause as cited by the latter.

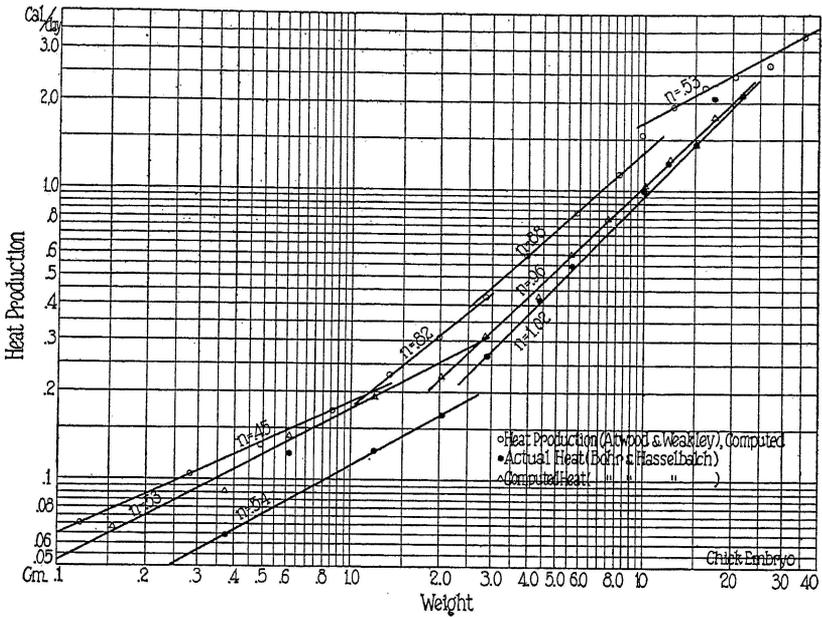


Fig. 37a.—The values of the exponents in the relation between heat production and body weight of the chick embryo appear to vary from .5 to 1.0.

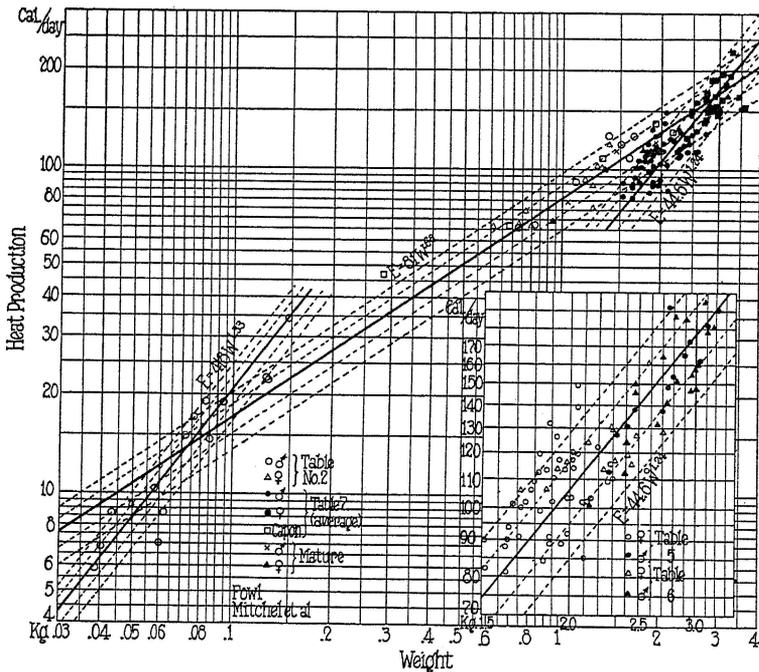
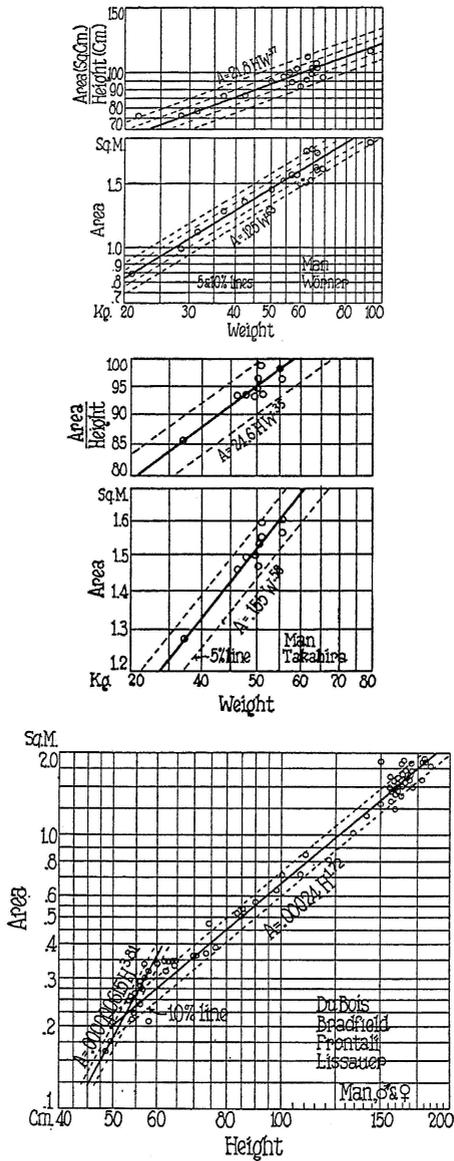


Fig. 37b.—The relation between heat production and body weight in the fowl. If heat production were proportional to surface area during the whole period of growth the values of the exponent, n , would be 0.67. The values of the exponents vary from 0.68 to 1.3.



Figs. 38a. to 38c.—The relation of area, A , to body weight, W , and to height, H or L , in man.

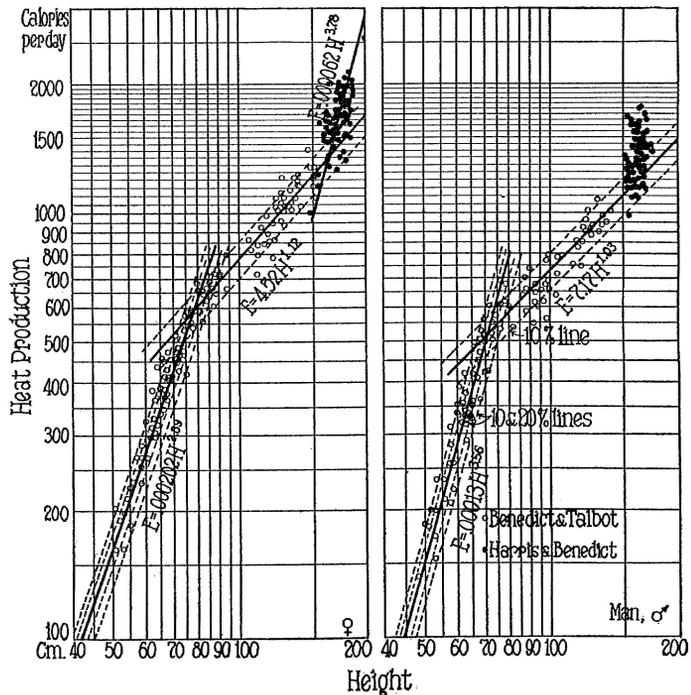


Fig. 39.—The relation of heat production to height. Between birth and one year heat production is proportional to the cube of the height; between 1 and 14 years, heat production is proportional to height. Following about 14 years, heat production is, in normally built individuals, nearly independent of height. Compare this chart with Fig. 11b in Research Bulletin 104.

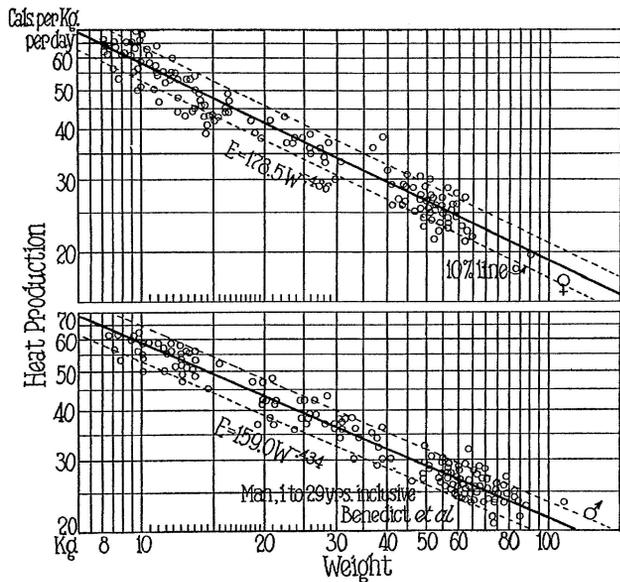


Fig. 40.—The heat production per unit weight for different weights between ages 1 and 29 years. Plotted from data by Benedict and associates (Carnegie Publications 302 and 279).

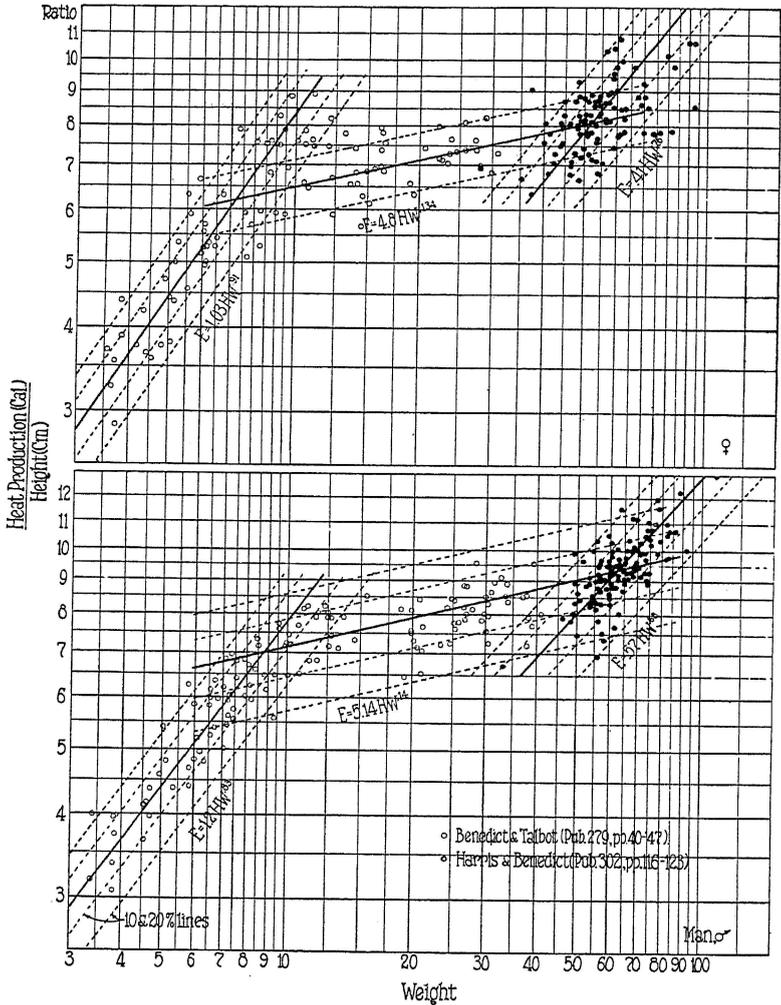


Fig. 41.—The relation of heat production, E, to weight, W, and to height, H, (compare to Figs. 39 and 12a). An incidental fact made clear by this chart is that heat production by a normal individual may vary by 20 per cent from the average for the population. Compare this chart with Fig. 11b in Research Bulletin 104.

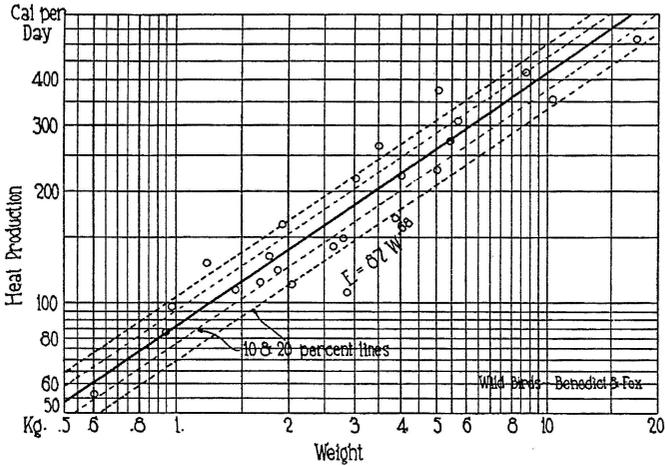
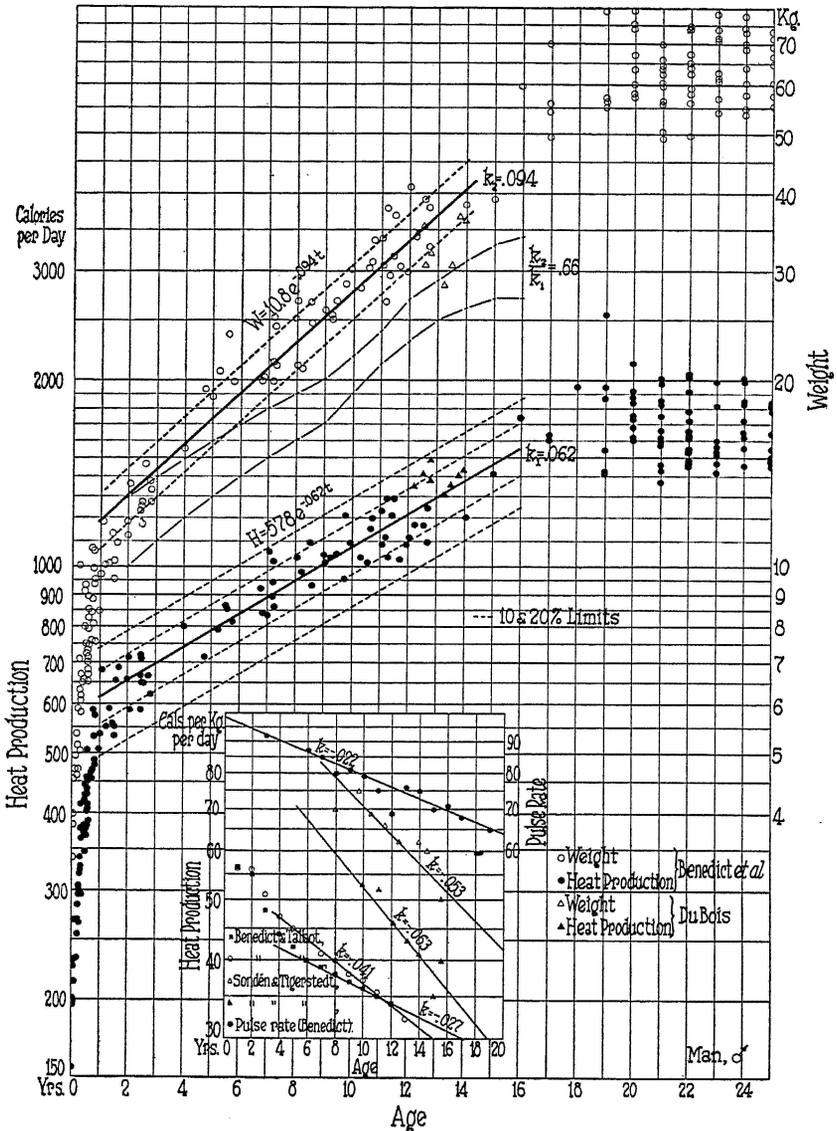
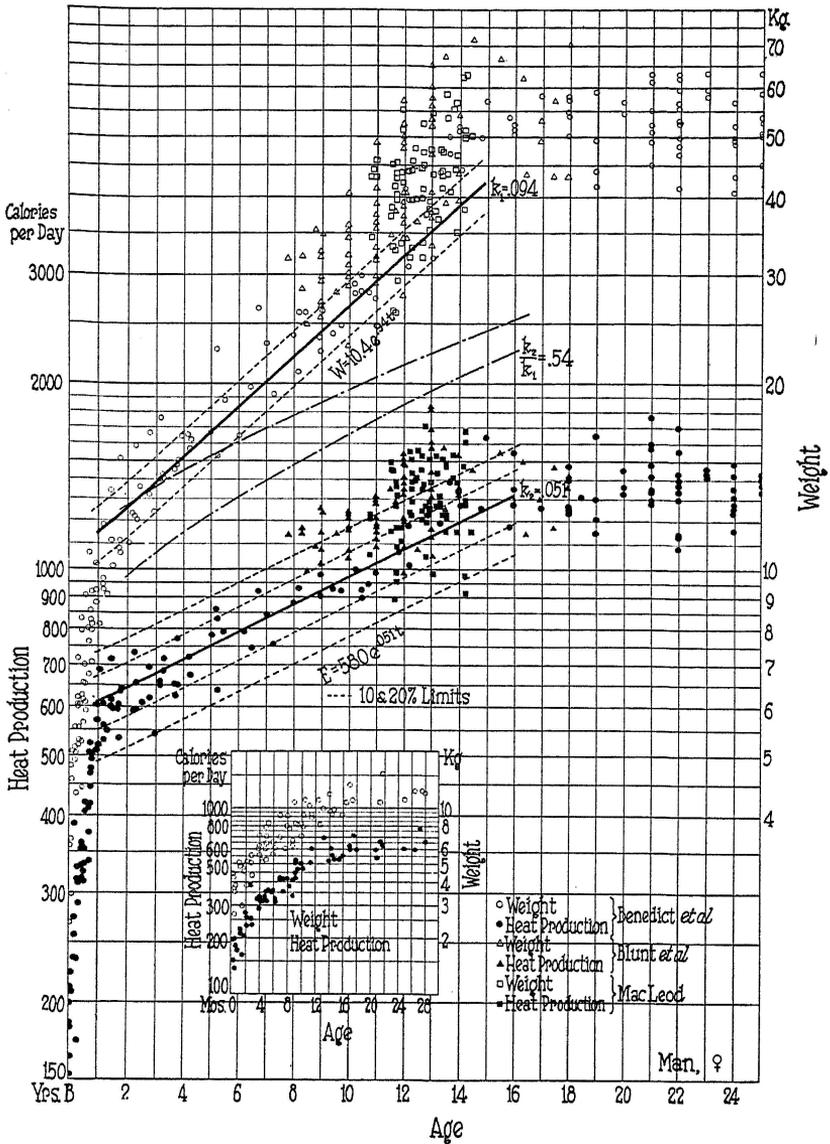


Fig. 42.—The relation between heat production, E , and body weight, W , of large wild birds. Plotted from data by Benedict and Fox (Proc. Am. Phil. Soc., 1927, LXVI, 511). The birds included, and their weights in kilograms, are as follows: Cassowary, 17.6; Condor, 10.3; Trumpeter swan, 8.9; Javan adjutant, 5.7; Jabiru, 5.5; Black-backed pelican, 5.1; Bearded vulture, 5.1; Paradise crane (4.0); Sandhill crane, 3.9; Brown pelican, 3.5; European flamingo, 3.0; Chilean sea eagle, 2.9; Curassow, 2.8; Black-necked screamer, 2.6; Purple guan, 2.0; Mexican blue heron, 1.9; Mexican blue heron, 1.9; Mexican blue heron, 1.8; Mexican blue heron, 1.7; Great horned owl, 1.45; Pacific gull, 1.21; Chilean skua, 0.97; White ibis, 0.94; American bittern, 0.60.



Figs. 43a and 43b.—Body weight, W , and heat production, H , of same individuals plotted against age on an arithlog grid. In chart inset for males a comparison is made between decline in heat production per unit weight with increasing age, and the decline in pulse rate. The pulse rate appears to decline one-half as rapidly as the heat production. Between the ages of 2 and 15 years body weight increases at the rate of 9 per cent per year (upper curve) while heat production increases at 6 per cent per year (lower curve). That is to say, the increase in heat production is about .66 of the increase in body weight for the males; for the females, it is .54 as great. The dash-and-dot curves represent the total energy needs



of children as estimated by Gillette. The data for males do not show the presence of a pubertal acceleration in heat production. The data by Benedict *et al* for females do not show a pubertal acceleration for heat production. The high values for heat production between 12 and 14 years for the females are based on data by Blunt and MacLeod and it is not fair to draw conclusions concerning this matter from data obtained by different investigators and on different children (the children measured by Blunt and MacLeod are heavier than those measured by Benedict *et al*) and by different techniques.

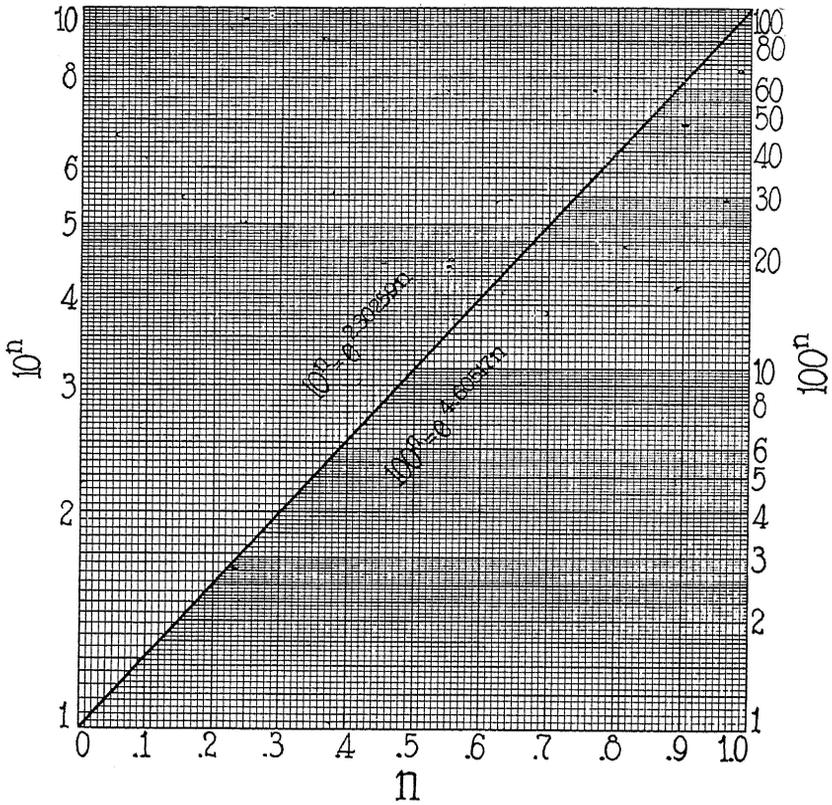


Chart B.—This chart is presented to enable anyone to determine the formula of a power function relating area to weight (or heat production to weight). The exponent, n , in the function

$$Y = C X^n$$

is the slope of the line on a logarithmic grid. This can be determined with a pair of dividers. The coefficient, C , is the value of Y when $X = 1$. If the value for $X = 1$ is not on the chart, then it may be determined by reading the value of X^n for $n = 10$, or $X = 100$ from this chart B, and solving for

$$C = \frac{Y}{X^n}$$