VOL. 6 JANUARY, 1932 NO. 11

HILGARDIA

A Journal of Agricultural Science

PUBLISHED BY THE

California Agricultural Experiment Station

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Body Size and Metabolism

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UNIVERSITY OF CALIFORNIA PRINTING OFFICE
BERKELEY, CALIFORNIA

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HILGARDIA

A JOURNAL OF AGRICULTURAL SCIENCE

PUBLISHED BY THE

CALIFORNIA AGRICULTURAL EXPERIMENT STATION

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BODY SIZE AND METABOLISM

MAX KLEIBER[1]

INTRODUCTION

The statement that the basal metabolism of animals differing in size is nearly proportional to their respective body surfaces, is called the surface law.

Benedict has shown that this law is already over ninety years old, Robiquet and Tillaye having formulated it quite clearly in 1839. The history of the surface law is given in the paper of Harris and Benedict (1919). We may here only briefly mention the different ways in which it has been found. The early writers derived the law from theoretical considerations on a rather small experimental basis, as did Bergmann, who in 1847 had already written a book on the subject. Respiration trials were carried out by Regnault and Reiset, and Rameaux based the surface law on measurements of the amount of air respired per minute by two thousand human beings of different sizes. Rubner (1883) demonstrated the law in accurate respiration trials on dogs and Richet rediscovered it empirically on rabbits. The latter writes (p. 223): "C'est *après coup* seulement que je me suis avisé que la donnée *surface* était plus intéressante que la donnée *poids*."

Although Armsby, Fries, and Braman (1918, p. 55) found the surface law confirmed to a rather striking degree, this law is not at all so clear today as it appeared to its early discoverers. Carman and Mitchell (1926, p. 380) state the situation very well: "In spite of the theoretical weakness of the surface law, the computation of basal metabolism to the unit of the body surface seems at present the most satisfactory method available of equalizing experimental results for differences in the size of experimental animals."

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This is probably the point of view of most physiologists: they feel the necessity of having a method which allows the reduction of the metabolism of animals different in size to a common basis to make the results comparable for studies of other influences on the metabolism. The surface law offers such a common basis, but the theoretical weakness of this law is recognized.

It is obvious that the scientist should strive to overcome any theoretical weakness; that purpose is one of the essential stimuli for research. But, also, if the law between body size and metabolism were only considered as a means for equalizing results and estimating food requirements, it would still be important to get rid of the theoretical weakness of the method, because this weakness may mean a wrong application also.

Harris and Benedict (1919) based their critique of the surface law upon the classical investigation of the Carnegie Nutrition Laboratory on human metabolism. They separated the interspecific point of view from the intraspecific and came to the conclusion that within the human species there is no evidence of that law; DuBois (1927, p. 202) on the contrary, on the basis of the same experiments, finds the law confirmed.

The situation is therefore that the critique of the surface law based on material within the human species has not given definite results on the question of the validity of that law. Benedict himself approves of the application of the surface law for comparisons between species. Benedict and Ritzman (1927, p. 153) write: "The method of comparison is, however, justified on the basis of usage, provided a false significance is not attached to it and that a causal relation between body surface and heat production is not insisted upon."

In this paper the surface law, its theory and its application, is discussed mainly from the interspecific point of view. It may be claimed as a working hypothesis that there is a general influence of body size on the metabolism, an influence upon which the other influences on metabolism are superimposed. In order to study the general influence of size, animals as different in size as possible should be chosen so that this influence of size may predominate over the other influences.

EMPIRICAL RESULTS OF RECENT WORK ON METABOLISM

The surface law is illustrated by Voit's table (Voit, 1901, p. 120) which has received wide publication (Krogh, 1916, p. 142; Lusk, 1928, p. 123). From this table it follows that the basal metabolism of all animals is close to 1,000 Cals. per 24 hours per square meter of body surface. Recent determinations, however, show considerable deviation

TABLE 1

BASAL METABOLISM PER SQUARE METER OF BODY SURFACE AND PER UNIT OF POWERS OF BODY WEIGHT

Group No.	Animal	W Average weight, kilograms	Cals. per 24 hrs. per animal	Formula for surface area	Heat production in 24 hours in Calories per unit of: Body surface (sq. meter)	$W^{2/3}$	$W^{0.7}$	$W^{0.73}$	$W^{0.74}$	$W^{0.75}$	$W^{0.76}$	$W^{0.77}$	$W^{0.8}$	W
1	Steer	679	8,274	$0.1081 \times W^{5/8}$	1,300	107.1	86.3	71.0	66.3	62.2	58.3	54.6	44.8	12.2
2	Steer	342	6,255	$0.1081 \times W^{5/8}$	1,465	127.9	105.5	88.5	83.5	79.2	74.2	70.0	58.8	18.3
3	Cow	388	6,421	$0.1081 \times W^{5/8}$	1,387	120.7	99.1	82.8	77.9	73.6	69.2	65.2	53.2	16.5
4	Man	64.1	1,632	$71.84 \times W^{0.425} \times L^{0.725}$*	926	101.9	88.7	78.3	75.1	72.0	69.1	66.3	58.5	25.5
5	Woman	56.5	1,349	$71.84 \times W^{0.425} \times L^{0.725}$	848	91.6	80.1	71.0	68.2	65.5	63.6	61.1	53.5	23.9
6	Sheep	45.6	1,219.9	$0.124 \times W^{0.561}$	1,163	104.8	84.1	74.9	72.1	69.4	66.8	64.3	57.3	26.7
7	Male dog	15.5	525	$0.112 \times W^{2/3}$	776	84.5	77.2	70.8	69.1	67.2	65.4	63.6	58.5	33.8
8	Female dog	11.6	443	$0.112 \times W^{2/3}$	772	86.5	79.7	74.0	72.2	70.5	68.8	67.1	62.4	38.2
9	Hen	1.96	106	$5.86 \times W^{0.5} \times L^{0.6}$	676	67.7	66.2	65.0	64.2	63.8	63.6	63.1	61.8	54.1
10	Pigeon	0.300	30.8	$0.0985 \times W^{2/3}$	697	68.7	71.5	74.1	75.0	75.9	76.9	77.8	80.6	102.6
11	Male rat	0.226	25.5	$0.1136 \times W^{2/3}$	600	68.7	72.2	75.4	76.6	77.7	79.0	80.1	83.9	112.9
12	Female rat	0.173	20.2	$0.1136 \times W^{2/3}$	572	65.1	68.9	72.7	74.0	75.3	76.6	78.0	82.4	116.6
13	Ring dove	0.150	19.5	$0.0985 \times W^{2/3}$	701	69.1	73.6	77.9	79.4	80.9	82.5	84.0	88.9	130.0
	Average of all 13 groups, Calories:				914	89.6	81.0	75.1	73.3	71.8	70.3	68.9	65.0	54.7
	Average of 9 groups (excluding ruminants), Calories:				730	78.2	75.3	73.2	72.6	72.1	71.7	71.2	70.1	70.8
					per cent	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*
	V, Coefficient of variability,† 13 groups, per cent:				±33.7	±23.9	±14.3	± 7.9	± 7.6	± 8.1	±10.0	±12.5	±21.5	±80.2
	V, Coefficient of variability, 9 groups, per cent:				±16.0	±16.9	± 9.1	± 5.6	± 6.5	± 8.2	±10.0	±12.1	±19.4	±61.9
	r, Coefficient of tendency,‡ 13 groups, per cent:				+ 0.215	+ 0.163	+ 0.088	+ 0.024	+ 0.002	− 0.031	− 0.042	− 0.064	− 0.132	− 0.506
	r, Coefficient of tendency, 9 groups, per cent:				+ 0.701	+ 0.808	+ 0.355	− 0.056	− 0.187	− 0.328	− 0.456	− 0.593	− 1.003	− 3.270

* L = Body length. † V = Standard deviation in per cent of the mean. ‡ r = Term explained on p. 320.

Sources of data:

Group 1: *Benedict and Ritzman (1927)*: The value of 1,300 Cals. per square meter given in the summary (Moulton formula) was used, and the average weight of the two steers calculated from the table given by Benedict and Ritzman (p. 60).

Group 2: *Forbes, Kriss, and Braman (1927, p. 176, table 2)*: Average of 18 determinations on 4 steers, third to tenth day of fasting.

Group 3: *Forbes, Kriss, and Braman (1927)*: Average of 10 determinations on 4 cows, second to ninth day of fast.

Groups 4 and 5: *Harris and Benedict (1919, p. 57, 65, and 67)*: Average of 136 men and 103 women.

Group 6: *Ritzman and Benedict (1931, p. 31)*: Average of 7 determinations on 7 sheep lying 18 to 50 hours after food, 21° to 25° C.

Group 7: *Kunde and Steinhaus (1926, p. 129)*: Average of 10 determinations on 10 male dogs, 8.75 to 26.8 kilograms in weight, 18 to 20 hours after food.

Group 8: *Lusk and DuBois (1924, p. 213)*: Average of 16 determinations on 11 female dogs, 9.1 to 15.8 kilograms in weight.

Group 9: *Mitchell and Haines (1927, p. 932)*: Average of 44 determinations on 14 hens of 1.63 to 3.51 kilograms weight at 54° to 99° F in darkness.

Group 10: *Benedict and Riddle (1929, p. 523)*: Average of 3 determinations on 3 pigeons of pure race at 30° C; average of day and night runs.

Groups 11 and 12: *Mitchell and Carman (1926, p. 392)*: Average of results on 23 male and 18 female rats. Periods of rest only. 28° to 31° C.

Group 13: *Benedict and Riddle (1929, p. 523)*: Average of 21 determinations on 9 ring doves of pure race, at 30° C; average of day and night runs.

from this statement. The writer himself has found with an old rabbit a basal metabolism as low as 440 Cals. per 24 hours per square meter of body surface. Results of extensive work on basal metabolism which has been done in recent years in America are summarized in table 1.

The main objection to using a table such as this is that basal metabolism is not so well defined a term as might be desirable. As early as 1888, Hoesslin stated that there was no minimum metabolism of definite magnitude.

By observing certain rules, i.e., comparing animals under the same conditions, one may, however, obtain comparable results. The requirements to be observed are summarized by DuBois (1927).

It is difficult to tell exactly what the same conditions are for different animals: 24 hours after the last food, is for example, physiologically not the same for the steer as for the hen or the rat, also a certain environmental temperature may have a very different effect on a cow than on a pigeon.

Although it cannot be claimed that the results in table 1 have been obtained under the same conditions, there is nevertheless reason to believe that the animals compared in this table have all been studied in an environmental temperature above the so-called critical temperature, so that the metabolism is practically independent of variations in temperature. It must be admitted, however, that the question of the critical temperature is not entirely settled. The data in table 1 were obtained on mature individuals so that the influence of age should not be important. This statement may indeed still be open to some criticism. For example, it follows from a curve given by Benedict and Macleod (1929, p. 381), showing the influence of age on the heat production of female albino rats, that the rate of metabolism per square meter of body surface increases in these animals with increasing age, namely from 650 Cals. for rats of 8 months to 900 Cals. for rats which are 24 months old.[2] These data were obtained at an environmental temperature of 28.9° C. There is further reason to assume that in all cases summarized in table 1 the after-effect of food is excluded or at least does not seriously affect the result.

Differences in the degree of motility may have an influence on the figures of table 1 and may be partly responsible for the especially high rates of metabolism in ruminants compared with the other animals. The metabolism of the rats, for example, is taken only from the periods in which the rats were quiet; periods of activity were excluded. The influence of differences in motility cannot, however, change the general

[2] These authors calculated the surface area according to the Meeh formula: $S=9.1W^{2/3}$ (p. 361).

result; for Benedict and Ritzman (1927, p. 229) state that rarely more than 15 per cent difference in metabolism was found for the maximum difference in activity of their steers. The relatively low value of the hen may be in connection with the fact that the determinations had been made in darkness.

A rough comparison of the column giving Calories per unit of body surface with the column giving Calories per unit of W on the one hand and the column giving Calories per animal on the other may be taken as a confirmation of the opinion of Lusk and of Armsby: By calculating the rate of metabolism to the unit of body surface, one obtains much closer results than by calculating it to either the unit of body weight or to the whole animal as a unit.

The coefficient of variability in the calculation of the metabolism to the unit of body surface is ± 34 per cent. Although this coefficient is not even half of that resulting from the calculation to the unit of body weight, it seems at first that with such a variability one must deny the validity of the surface law as Benedict (1915, p. 277) has done.

A high coefficient of variability as such, however, is not sufficient reason to refute a suggested law. If the same deviations from the mean as those of the Calories per square meter in table 1 were so distributed among the different groups that the averages of six groups of the larger animals as well as the averages of six groups of the smaller animals would differ less than, say, 14 per cent $\left(\frac{34}{\sqrt{6}}\right)$ from the total average there would be reason to expect that with a material of six hundred instead of six groups on each side the difference of the means of each half from the total average might be within ± 1.4 per cent and that with increasing number of groups the average metabolism per square meter of large animals might be found more and more nearly the same as the corresponding average of small animals. If the deviations were so distributed there would be reason to expect that with increasing number of groups the surface law (the theory that the heat production per square meter of body surface is the same for large and small animals) could be proved with increasing accuracy and then the title of "law" would be justified in spite of the coefficient of variability of ± 34 per cent.

More serious for the surface law than the high coefficient of variability is the fact that the metabolism per square meter in table 1 shows a pronounced tendency to be increased with increasing size of the animal. If the results are grouped in two halves (omitting the middle group 7) six representing the larger and six the smaller animals the average heat production per square meter of the large animals is 512 Cals. or 56

per cent of the total average higher than the average for the small animals. In order to obtain a measure for the tendency of the metabolism to be increased with increasing body size the difference between the half averages in Calories has been divided by the corresponding difference in weight as shown in the following calculation:

Group No.	Average heat production per square meter $\overline{M}$	Difference $\Delta\overline{M}$	Average weight $\overline{W}$	Difference $\Delta\overline{W}$
	Cals.	*Cals.*	*kg*	*kg*
1– 6	1,182	512	262.5	260.1
8–13	670		2.4	

Thus $\frac{\Delta\overline{M}}{\Delta\overline{W}} = \frac{512}{260.1} = 1.97$ Cals. per sq. meter per kg.

The basal metabolism per square meter increases 1.97 Cals. per kilogram increase in body weight. As the average basal heat production is 914 Cals. per square meter, the increase per kilogram increase in body weight is 0.215 per cent of the mean. This is the coefficient of tendency τ in table 1.

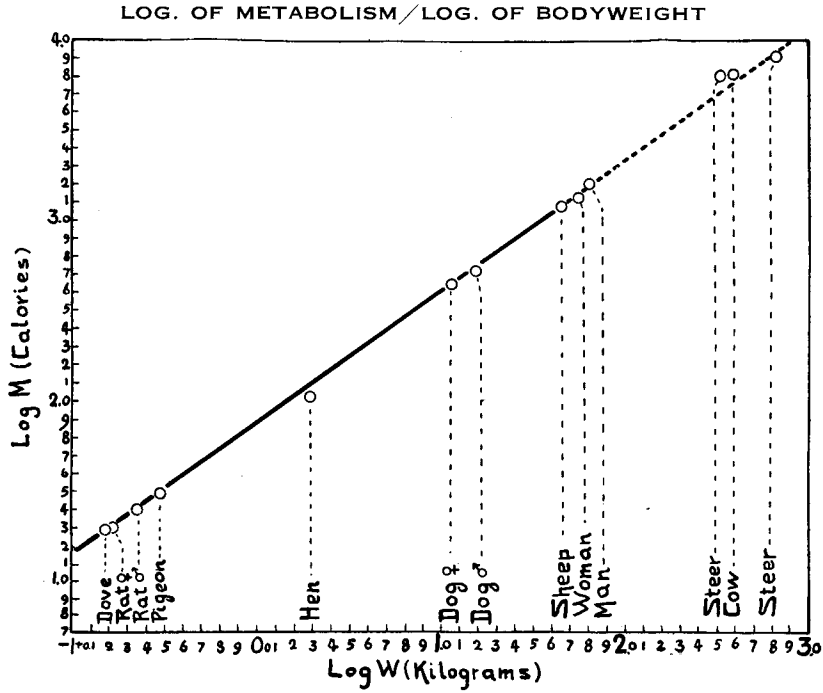
The metabolism of the thirteen groups of animals has also been calculated to the unit of different powers of the body weight (W). The distribution of the deviations from the mean is best (τ is minimum) if the metabolism is calculated to the 0.74 power of the body weight. In this case the coefficient of variability is ± 7.6 per cent.

By excluding the ruminants from the calculation the deviation may be decreased. In this case the coefficient of variability is ± 16.0 per cent if the metabolism is calculated per square meter of body surface and as low as ± 5.6 per cent if the 0.73 power of the body weight is chosen as unit. If the different types of animals grouped together and the large range in body size are considered, it is surprising that any formula can be found which gives such a relatively low coefficient of variability.

A general formulation of the law expressing the relation between body size and metabolism may be found if the logarithm of the metabolism is plotted against the logarithm of the body weight; this has been done in figure 1. A straight line results, indicating that *the logarithm of the basal metabolism is proportional to the logarithm of the body weight.*

By differentiation of this function one finds that a small increase in metabolism per unit of the corresponding increase in body weight is proportional to the metabolism per unit of body weight:

$$\frac{dM}{dW} = K\frac{M}{W}$$



It also may be expressed that the relative rate of increase of metabolism is proportional to the relative rate of increase in body weight:

$$\frac{dM}{M} = K\frac{dW}{W}$$

It follows from the linear function of the logarithms of metabolism and body weight that the metabolism per unit of a certain power of the body weight is constant. This, indeed, is no other result than was obtained by trying different calculations in table 1 and finding that the $\frac{3}{4}$ power of the body weight was the best-fitting unit.

It must be admitted that the material, though without doubt superior to that used heretofore as a basis for the surface law, is not yet homogenous and not adequate enough to decide conclusively to which power of the body weight (between the $\frac{2}{3}$ and the $\frac{3}{4}$) the general influence of body size on the metabolism is most closely related. Two conclusions with regard to the surface law from the interspecific point of view may, however, be drawn:

1. The surface law is *confirmed* insofar as one gets closer results by calculating the basal metabolism to the unit of body surface than by calculating it to the unit of body weight.

2. The surface law is *refuted* insofar as the calculation of the metabolism to the unit of a power function of the body weight gives as close results as the calculation to the unit of body surface, or even closer.

THE THEORIES OF THE RELATION BETWEEN BODY SIZE AND METABOLISM

The question is now whether, on the basis of the material in table 1, the surface law should be abandoned and a weight-power law for the metabolism postulated, or whether there is reason to assume that the empirical result from table 1 is insignificant compared with the theoretical evidence of the surface law. To this end the amount of evidence for the statement that the metabolism is proportional to the body surface should be studied.

Four different theories which have been put forward to explain the surface law on physical or chemical bases may be distinguished, and then a biological explanation of the relation between body size and metabolism formulated.

Surface Law and Temperature Regulation.—The amount of heat required to maintain a constant temperature in a warm body surrounded by a cooler medium is proportional to the surface of that body. This has been, and still is designated in physiological papers, as the application of Newton's cooling law, although Harris and Benedict (1919, p. 135) have already criticized this terminology.

Newton's law of cooling may be written as follows:

$$\frac{du}{dt} = \frac{1}{k}(u_1 - u_2)$$

In a body with the temperature u_1 surrounded by a medium of the temperature u_2, the loss of temperature (du) per unit of time (dt) (rate of cooling) is proportional to the difference in temperature inside and outside. As the animal keeps the inside temperature constant, du becomes 0, and the law loses its application. There is no cooling, but heat flow.[3] The architect (Hütte, 1925, vol. 3, p. 335), in order to estimate the size of a furnace needed for a house, can calculate heat flow from inside to outside on the basis of Fourier's formula (Mach, 1919, p. 84):

[3] It may be mentioned that at Newton's time the two conceptions of temperature and heat were not kept clearly separated one from the other. (Mach, 1919, p. 132).

$$H = k \times O \frac{u_1 - u_2}{L} t$$

H = heat passed (calories)
k = coefficient of thermal conductivity
O = cross-section area of thermal conductor
L = length of thermal conductor
$u_1 - u_2$ = difference in temperature for the length L
t = time

This formula, originally derived for the flow of heat within a conductor may, as the application of the architect shows, be used for the calculation of the heat transmission entirely through a conductor.

For application to the problem of body metabolism, the surface area of an animal would be taken as the cross-section area and the thickness of the body covering as the length of the conductor.

The body covering of an animal includes the hair, the air in the interstices between the hair, the skin, the subcutaneous fat, and perhaps additional tissues (Benedict and Ritzman, 1927, p. 143; Benedict and Slack, 1911, p. 35).

The thermoconductive thickness, i.e., the thickness representing a certain average conductivity, of this cover is difficult to define. The situation may be simplified by introducing the term *specific insulation* of the animal and defining it as:

$$r = \frac{L}{k}$$

where r = specific insulation (resistance against heat flow)
L = the thermoconductive thickness of the cover
k = the average heat conductivity of the cover.

The following formula can then be derived:

$$\frac{H}{Ot} = \frac{u_1 - u_2}{r}$$

where $\frac{H}{Ot}$ = heat flow per unit of surface per unit of time (in the following tables given as small calories per square centimeter of body surface per day)
$u_1 - u_2$ = the difference in temperature inside and outside the covering, given in °C
r = the specific insulation

H means here the part of the total heat loss of the animal which passes through the skin. For an approximation, the total heat loss may be substituted for H and the additional amount resulting from heat

loss by other ways than the skin—especially the amount of heat given off through the respiratory organs—neglected. At abnormally high outside temperatures where the animal uses polypnoe as a means to prevent overheating the neglecting of the heat loss through the respiratory system might introduce a considerable error. The expression $u_1 - u_2$ means the difference in temperature inside and outside of the animal's covering. For an approximation, u_2 may be taken as equal to the temperature of the environmental air. At high outside temperature, however, the temperature of the skin may be considerably lower than that of the surrounding air (because of evaporation of water and radiation). This fact, like that first mentioned, tends to decrease the reliability of the approximation for high outside temperatures.

The data in table 2 have been derived from my own earlier experiments.[4]

TABLE 2

SPECIFIC INSULATION OF RABBITS

Animal	Temperature, °C	$u_1 - u_2$, °C	$\frac{H}{Ot}$	r
Old rabbit	18	22	49.7	0.44
	13	27	53.8	0.50
	4	36	72.7	0.50
Young rabbit	21	19	66.7	0.28
	13	27	74.4	0.36
	3	37	86.0	0.43

The specific insulation of the old rabbit remains fairly constant, but the young rabbit increases its insulation against heat loss with decreasing outside temperature. These results would seem to indicate that the young animal has a wider range of physical temperature regulation (regulation of blood circulation in the skin and the condition of fur).

Using data from Benedict and Ritzman (1927, p. 219) the calculations given in table 3 with regard to steers may be made:

TABLE 3

SPECIFIC INSULATION OF STEERS

No.	u_2, °C	u_1, °C	$u_1 - u_2$, °C	$\frac{H}{Ot}$	r
1	2.9	37.7	34.8	174	0.200
	24.9	37.7	12.8	106	0.121
2	8.8	37.7	28.9	185	0.156
	28.3	37.7	9.4	119	0.079
3	3.4	37.7	24.3	173	0.198
	28.2	37.7	9.5	129	0.074
4	27.9	37.7	9.8	161	0.061
	7.3	37.7	30.4	145	0.210

[4] Carried out in the Swiss Institute for Animal Nutrition, Zurich.

The results show that steers can adapt their specific insulation considerably to the environmental temperature. In No. 4, where the steer had been first at high and then at low temperature, the regulation of the specific insulation was so pronounced that the animal had a reversed chemical regulation and produced less heat at low than at high environmental temperature.

Substantially the same results may be calculated from data on sheep published recently by Ritzman and Benedict (1931, p. 26, table 9).

TABLE 4

SPECIFIC INSULATION OF SHEEP

No.	Temperature, °C			$\frac{H}{Ot}$	r
	Outside (u_2)	Body (u_1)	u_1-u_2		
1	3.4	39.2	35.8	129	0.277
	5.8	39.2	33.4	131	0.255
	23.3	39.2	15.9	153	0.104
2	8.7	39.4	30.5	109	0.280
	11.5	39.4	27.7	112	0.247
	27.5	39.4	11.7	117	0.100
3	3.2	39.4	36.0	131	0.275
	9.2	39.2	30.0	154	0.195
	30.7	39.2	18.5	172	0.049*
4	−0.1	39.2	39.3	121	0.325
	20.8	39.2	18.4	120	0.153

* Two days before lambing

The reversed chemical temperature regulation occurs in three of four cases in these experiments with sheep.

A behavior opposite to that of the one steer and the three sheep, namely a strict action of the chemical temperature regulation in Rubner's sense and even a reversed physical regulation may be calculated from data on fasting experiments with eight female albino rats published recently by Horst, Mendel, and Benedict (1930, tables 4 and 5). The calculation is presented in table 5.

TABLE 5

SPECIFIC INSULATION OF RATS

Day of fast	Activity	Temperature, °C			$\frac{H‡}{Ot}$	r
		Outside (u_2)	Body† (u_1)	u_1-u_2		
1*	15	16	37.5	21.5	126	0.171
1	16	26	37.5	11.5	66	0.174
7	28	16	37.5	21.5	123	0.175
7	10	26	37.5	11.5	50	0.230

* 22 hours without food.

† The body temperature, not found in the paper, has been supplied from direct measurements.

‡ The surface is calculated according to Meeh, $O = 9.1\,W^{2/3}$.

At the beginning of the fast the specific insulation of the rats at high and low environmental temperature was essentially the same. At the seventh day of fast the rats at high temperature had even a higher specific insulation than the rats at low outside temperature. The difference is such that it does not seem reasonable to explain it as within the errors of experiment or calculation, as, for example, due to the use of a constant body temperature. Some clue for an explanation may be found in the fact that activity was decreased during prolonged fasting at high outside temperature but was increased with prolonged fasting at the low outside temperature.

From earlier data of Benedict and Macleod (1929, p. 369, fig. 1), results on rats which confirm those obtained on steers, sheep, and rabbits may be obtained, as shown below:

Temperature, °C		$\frac{H}{Ot}$	r
Outside (u_2)	$u_1 - u_2$		
10	27.5	180	0.153
28	9.5	88	0.108

That the animal can change its insulation has been clearly demonstrated by Hoesslin (1888, p. 329). He raised two dogs from the same litter, one at 32° C and the other at 5° C, and found from the different amounts of body substance produced by these two dogs, considering the amount of food consumed, that the one at 5° C had a metabolism only 12 per cent above that of its brother. Hoesslin states that if the heat loss had been the determining factor for the rate of metabolism (assuming a constant specific insulation), the difference in metabolism should have been several hundred per cent. The explanation was found in the fact that at the end of the 88 days of the trial the hair of the dog kept at 5°C weighed 129 grams, that of the other only 36 grams.

In a strict sense the surface law could be explained on the basis of Fourier's formula for the heat flow only if the specific insulation in small and large animals were the same. This situation cannot be expected, for it has just been shown that the insulation changes even in the same animal according to different outside conditions. It would not, however, be correct to discard the heat-loss theory entirely, as is often done.

The possibility of changing the specific insulation is actually limited. For example, steer *C* of Benedict and Ritzman (1927), which weighed 600 kilograms, had at an environmental temperature of 2.9° C a specific insulation of 0.200. If, for purposes of discussion the same heat conduc-

tivity is assumed for the body covering of the steer as has been found for the rabbit fur by Rubner (1895, p. 380), namely 6×10^{-5} calories per second, or 5 calories per 24 hours per square centimeter with a temperature gradient of 1° C per centimeter, the thermoconductive thickness[5] of the steer cover is found to be 1 cm. (According to the definition of the specific insulation given on page 323, it follows: $L=rk=0.2\times5=1.0$.)

A mouse of 60 grams with the same heat production per unit of body weight and the same heat conductivity of the cover would require a thermoconductive thickness of covering of no less than 20 cm to keep its body temperature at the same level above the outside temperature as does the steer.[6] The fact is that the mouse produces 20 times as much heat per gram of body weight as does the steer, and animals of the size of a mouse would not be able to live as warm-blooded animals in the temperate and cold zones of the world if they had only the same rate of heat production per unit of body weight as a steer.

The heat-loss theory of the surface law is thus reasonable if one compares animals very different in size which are living at relatively low temperatures.

The heat-loss theory loses its application for explaining the surface law in animals which are living in warm climates where they have to operate regulating systems to get rid of a surplus of heat. The ability to give off heat and prevent overheating was, however, also related to the surface law by Rubner in 1902 (Lehmann, 1926, p. 575). The same statement can be made for the overheating theory as for the heat-loss theory, namely, that it does not apply to animals of similar size, but is reasonable if the animals compared differ considerably in size.

The sailors whom Robert Mayer had to bleed on board the ship "Java" in the Bay of Surabaya in the summer of 1842 had light red venous blood, a fact which led that young genius to the discovery of the law of conservation of energy. The blood was light red because the sailors had decreased their muscular activity in the hot zone in

[5] Defined on p. 323.

[6] The surface per unit of body weight, which in an animal is practically the same as the surface per unit of body volume, or the specific surface, is $\frac{W^{2/3}}{W}=W^{-1/3}$. The ratio of the specific surfaces of mouse to steer is thus the cube root of the inverse ratio of their respective body weights $\sqrt[3]{\frac{600\times10^3}{60}}=10\sqrt[3]{10}=21.6$. The surface per gram of mouse is therefore 20 times as large as the surface per gram of steer. With the same heat production per gram of body weight, the heat flow through 1 sq. cm of surface of a mouse should therefore be only 1/20 of that through 1 sq. cm of surface of a steer; consequently the specific insulation of the mouse should be 20 times as high as that of the steer.

order to prevent overheating. What would they have done with a heat production ten times as great, which per unit of body weight would correspond to the metabolism of a mouse? If animals varying much in size and living in hot regions are considered, the overheating theory of the surface law is thus acceptable.

For hot as well as for cold climates, therefore, the maintenance of a constant body temperature gives us a sound explanation for the surface law if animals of considerably different size are compared; this is an explanation only in the sense, however, that the regulation of body temperature is not the cause, but one of the conditions which influence the metabolism and is therefore a criterion, among others, in the selection of the fittest.

Surface Law and Nutritive Surfaces.—Puettner (Lehmann, 1926, p. 577), using older ideas such as those of Hoesslin, has stated that the surfaces of the intestinal tract and of the lungs and, finally, the surfaces of the individual cells of the animal are the important factors for the rate of metabolism, and that one may explain the surface law as resulting from the rate of diffusion of the nutrients through these internal surfaces.

Pfaundler (1921, p. 273) states correctly that the surfaces of the cells could be responsible for the surface law only if the cells in an animal merely grew but did not increase in number, because only in this case could the sum of the cell surfaces in an animal be proportional to its body surface. Pfaundler himself, however, attempts to explain the surface law basing his explanation on Buetschli's theory of the structure of the protoplasm, the "Wabenstruktur" (honeycomb structure). Pfaundler apparently believes that the sum of the surfaces of those hypothetical structures of the living substance in an animal should be proportional to the $\frac{2}{3}$ power of the body weight. This would imply that the protoplasmic elements of a man in linear dimensions should be ten times as large as the corresponding elements of the protoplasm of a mouse; or that one kilogram of protoplasm of an ox should contain the same number of protoplasm units as one gram of guinea pig plasm. It is doubtful whether any real basis can be found for such a logical consequence of Pfaundler's theory.

The final refutation of all attempts to explain the surface law with cell and cell-structure surfaces comes as a result of the modern research on the respiration of tissues; according to Terroine and Roche (1925), *homologous tissues of different animals have in vitro the same intensity of respiration.*

In the same year Grafe (1925) states: "The living protoplasma of the warm-blooded animals and maybe even of many cold-blooded

animals, shows as far as the respiration is concerned a certain uniformity and gets its specificity only by means of the influence of the regulating system of the animal."

Grafe, Reinwein, and Singer (1925, p. 109) found some differences in the respiration of tissues of different animals in vitro. The average oxygen consumption per gram of dry matter per minute is 0.2 cc for mouse tissue and 0.119 cc for that of the ox. These authors state, however, that this difference cannot explain the fact that in vivo one gram of mouse body uses up per unit of time 33 times as much oxygen as one gram of ox body.

The law of body size and metabolism is therefore not a matter of the tissues, but a matter of the organism as a whole.

TABLE 6

BLOOD VOLUME AND BODY WEIGHT

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

Surface Law and Composition of the Body.—Benedict has shown (1915, p. 298) that the proportion of inert body fat and *active protoplasmic tissue* influences the metabolism. This influence may be as effective as that of size within the human species. An influence of this kind cannot, however, be used as an explanation for the surface law if animals of considerably different size are compared. Thus Carman and Mitchell (1926, p. 380) have calculated that if a rat consisted entirely of active protoplasm, then a man, with his lower metabolism per unit of weight, should on that basis contain only 9.4 kg of active protoplasm.

Dreyer, Ray, and Walker (1910, p. 158) suggested that the *blood volume* of an animal was proportional to the surface area of that animal and that "the practice of expressing the blood volume as a percentage of the body weight is both erroneous and misleading." The results of these last named investigators may be summarized in table 6.

Column 4 of table 6 shows that according to the formulas of Dreyer, Ray, and Walker the blood volume is to be calculated by multiplying the $\frac{2}{3}$ power of the body weight by a factor which varies directly with

the size of the animals, if different species are concerned. The blood volume per unit of $W^{2/3}$ in the rabbit is 4.2 times $\left(\frac{0.632}{0.149}\right)$ as large as that of the mouse. From column 5, on the other hand, it may be concluded that the blood volume per gram of body weight is not related to the size of the animals, i.e., that the blood volume is proportional to the body weight.

The theory of Dreyer, Ray, and Walker that the blood volume is proportional to the body surface (or the $\frac{2}{3}$ power of the body weight) must therefore be refuted on the basis of their own results, at least from the interspecific point of view.

Recently Brody, Comfort, and Matthews (1928, p. 33) as a result of extensive research and ingenious calculation,[7] have claimed that "the weight of the kidney, the weight of the liver, and practically the weight of the lung, blood, stomach, and intestine increase directly with the body weight at the same relative rate as does the surface." Their results (see their fig. 6, p. 17) indicate, however, that the surface area follows the function $W^{0.71}$ and the blood volume the function $W^{0.83}$.

If animals of very different size are compared, it can be seen that the blood volume cannot be proportional to the body surface, but must be related to a function which is not far from the first power of the weight.

It may be that the differences in the blood quantity per unit of body weight in any one species are affected by age and fat content. Possibly the heavier animals used are on the average older and fatter. This idea gains strength from the work of Trowbridge, Moulton, and Haig (1915, p. 16), who state in relation to cattle that "the fatter the animal the smaller the proportion of blood."

Lindhard (1926, p. 669) found the blood quantity of man (11 healthy subjects) to be 4.9 per cent of the body weight. If the blood quantity were proportional to the body surface, the 70-gram body of the rat should contain 34 cc of blood, or 49 per cent.[8]

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[7] Surface integrator measurements on 482 dairy cows, 341 beef cattle, 11 horses, and 16 swine.

[8] If W_m be the weight of man and W_r the weight of rat we may formulate:

$$\text{Blood volume of man per } W^{2/3} \text{ unit} = \frac{0.049\ W_m}{W_m^{2/3}}$$

$$\text{Blood volume of rat per } W^{2/3} \textit{ unit} = \frac{xW_r}{W_r^{2/3}}$$

If the blood volume were proportional to $W^{2/3}$, the two quotients would be equal, thus:

$$x = \frac{0.049\ W_m W_r^{2/3}}{W_m^{2/3} W_r} = 0.049\left(\frac{W_m}{W_r}\right)^{1/3} = 0.049 \times 1{,}000^{1/3} = 0.49 = 49 \text{ per cent.}$$

It follows thus that the surface law is not a matter of the tissues or cells and cannot be a matter of the chemical composition of the animal, but is a matter of the animal as a whole. The two great regulators, the nervous and endocrine systems, control the intensity of blood flow and the distribution of the blood to the tissues, so that the respiratory metabolism of animals of different size is approximately proportional to the $\frac{2}{3}$ power of the body weight.

Surface Law and Blood Circulation.—Loewy (1926, p. 22) has summarized data on the oxygen content of arterial and venous blood. It follows from his table that a liter of blood which passes the capillary system leaves on the average 60 to 70 cc of oxygen in the tissues, and further that this amount is independent of the size of the animal. It is therefore sound to assume that the amount of oxygen carried to the tissues per unit of time (intensity of oxygen flow) is on the average proportional to the amount of blood passing the tissues per unit of time (intensity of blood flow).

Hoesslin (1888) attempted to show that for geometrical and mechanical reasons the amount of blood carried to the tissues per unit of time must be proportional to the $\frac{2}{3}$ power of the body weight. He bases his reasoning on the assumption of the geometrical similarity of large and small animals. This geometrical similarity means that all dimensions which are in certain arithmetical ratios in small animals are in the same ratio in large animals. Thus, if the cross-section area of the aorta of a small animal be a per cent of the cross-section area of the body or b per unit of the $\frac{2}{3}$ power of the body weight, the aorta of a large animal also will have a cross-section area which is a per cent of the cross-section area of its body or b per unit of the $\frac{2}{3}$ power of the body weight. This assumption, especially with regard to the aorta, has really been fairly closely confirmed by measurements of Dreyer, Ray, and Walker (1912), who found that the cross-section area of the aorta is proportional to a function of the 0.70 to 0.72 power of the body weight.

The amount of blood passing a certain cross section of the body per unit of time is the product of the sum of the cross-section areas of all blood vessels in that body cross section and the linear velocity of the blood flow. The linear velocity is, according to Volkmann (Hoesslin, 1888, p. 324), independent of the size of the animal. Therefore, concludes Hoesslin, the product, the intensity of blood flow, is proportional to the sum of the cross-section areas of the blood vessels and is thus proportional to the $\frac{2}{3}$ power of the body weight, a suggestion which explains, according to him, also the fact that the metabolism is proportional to that power of the body weight.

As the capillaries of a horse are not ten times as wide as those of a guinea pig, but are of approximately the same size, it follows that the principle of similarity mentioned above applies only to the large vessels. Hoesslin's explanation of the surface law is therefore satisfactory only if we can understand why the linear velocity in the large vessels is independent of the body size.

The question may be related to the economy in energy consumption for blood circulation. The specific current energy, i.e., the energy necessary for the transport of 1 cc of blood through a given part of the duct, is higher for turbulent than for laminar flow, as has been stated by Hess (1927, p. 901). The same author demonstrated that under normal conditions the blood flows laminarily (1917, p. 477).

In certain pathological cases where the viscosity of blood is abnormally low, murmurings in the large vessels may be heard, which, according to Hess (1927*a*, p. 913) indicate that the normal velocity of blood flow cannot be far from the critical velocity, beyond which the flow would be turbulent.

According to Reynold (Hess, 1927, p. 900) the critical velocity is inversely proportional to the diameter of the duct.[9] If it were advantageous for the animal to maintain in its large vessels a velocity close to the critical, and if this advantage were the determining factor for the velocity of blood flow, one would expect, according to Reynold's formula, that the linear velocity of blood flow in animals of different size would be inversely proportional to the linear dimensions of the body or to the $\frac{1}{3}$ power of the body weight. This expectation is in contradiction to the constancy of the linear velocity of blood flow, instead of being an explanation for it.

Hoesslin's theory of the relation between surface law and blood circulation is thus less satisfactory than it might appear at a first glance (see for example Lehmann, 1926, p. 577).

For a schematical comparison of the blood circulation in small and large animals three groups of vessels should be distinguished:

1. The larger arteries and veins, which may be called the individual vessels. They are dependent in size (diameter and length) upon the body size of the animal. Their number is independent of the size of the animal.

[9] Reynold's equation for the critical velocity reads as follows:

$$v = \frac{2000\eta}{2rs}$$

v = critical velocity
η = viscosity of the fluid
s = density of the fluid
r = radius of the duct

2. A second group of vessels, represented by the capillaries, which may be termed the tissue vessels. Their size is independent of the size of the animal, but their number depends upon the amount of tissues and therefore upon the size of the animal.

3. The connecting vessels, which connect the system of the individual vessels with the capillary net work. The vessels of this group depend in size as well as in number upon the body size of the animal.

The amount of blood passing a cross section of the duct per unit of time is, for laminar flow, according to Poisseuille[10] proportional to the difference in pressure at the end of a given part of that duct and inversely proportional to the hemodynamic resistance. The hemodynamic resistance is proportional to the length and inversely proportional to the square of the cross section of the duct.

For the individual vessels, which may collectively be represented as a single vessel, the length is proportional to the $W^{1/3}$ and the cross section proportional to $W^{2/3}$. The hemodynamic resistance of this system is therefore proportional to $\frac{W^{1/3}}{W^{4/3}}$ or $\frac{1}{W}$.

The arterial blood pressure of animals is independent of the body size (Tigerstedt, 1921, p. 209). This may be expected from Hoesslin's point of view of the similarity of large and small animals, for it is a technical rule that pipes of different width in which the wall thickness is proportional to the diameter can stand the same pressure. (Hütte, 1925, vol. 1, p. 675.) If, however, in pursuance of this idea, it is assumed that there is the same difference in blood pressure for corresponding parts of the individual vessels of large and small animals, then according to Poisseuille's law the intensity of blood flow would be proportional to the body weight instead of being proportional to the $\frac{2}{3}$ power of this term.

The same result is obtained for the tissue vessels if it is assumed that the number of available capillaries is proportional to the amount of tissue, and hence to the body weight, and that the average length and width of each capillary are independent of the body size. It is difficult, if not impossible, to verify this assumption. The number of open (but

[10] The law of Poisseuille may be formulated as follows:

$V = \frac{q^2}{8\pi\eta L}\Delta P \times t$ where:

V = volume of liquid passing a certain part of the duct
q = cross section of duct
L = length of duct
ΔP = difference in pressure
t = time
π = 3.14 . . .
η = viscosity

not the number of available) capillaries which are counted under the microscope varies according to whether the muscle from which a part is observed has been in action or at rest before the animal was killed.

Krogh (1929, p. 63) counted in a section from a stimulated muscle of the frog 195 open capillaries per square millimeter, while the corresponding unstimulated muscle had not more than 5.

Krogh (1929, p. 30) found on the average fewer open capillaries per unit of cross section in tissues of a large animal than in those of a small one; the muscle of a horse (550 kg) had 1,400 capillaries per sq. mm, and the muscle of a dog (5 kg) had 2,600 capillaries per sq. mm. Terroine (1924) bases his theory of the relation between body size and metabolism upon this fact. The average number of open capillaries is, however, a result of the regulation of blood flow by the nervous and the endocrine systems and cannot therefore be used as an explanation for the regulation of blood flow to a certain level.

Less contradiction is to be found if the surface law is related to the rate of *heart beat*. The total blood volume in an animal is proportional to the body weight (see p. 330), and the blood volume moved by one heart beat is, in mammals, a constant part of the total blood volume, namely 1/26 to 1/29, according to Vierordt (cited by Kisch, 1927, p. 1218). The pulse rate in the mouse (*Mus musculus*) is 520 to 780 beats per minute, in man 76, and in the horse 34 to 50. A frequency of 300 to 400 would be classed as extreme tachycardia in man (Winterberg, 1927, p. 671). The contraction of the heart muscle in the horse requires 0.1 second (Tigerstedt, 1921, p. 209); the pulse rate of the mouse would mean tetanus in the heart of a horse. These facts indicate why the pulse rate should be inversely proportional to a function of the body weight in animals of widely different weights, but they give no satisfactory clue as to why this relation should obtain exactly between animals of closely similar size. The situation is similar to that between the surface law and temperature regulation (see p. 326).

The pulse rate reported for different individuals of the same species differs so considerably that it would seem at first glance almost impossible to determine an exact relation between pulse rate and body size. For an approximate estimate, however, the logarithmic method as used by Brody, Comfort, and Mathews (1928) may be applied on data for the pulse rate of elephant, horse, cattle, sheep, and rabbit given by Rihl (1927) and the relation of pulse rate and body weight reduced to the equation:

$$P = 186 \times W^{-1/4}$$

where P = pulse rate (beats per minute)
W = body weight in kilograms

In order to give an explanation for the surface law, the pulse rate should be proportional to the $-\frac{1}{3}$ power of the weight instead of the $-\frac{1}{4}$ power.

If the volume per heart beat were exactly proportional to the body weight and the pulse rate were exactly proportional to the $-\frac{1}{4}$ power of the body weight, the intensity of blood flow would be proportional to the $\frac{3}{4}$ power of the body weight. This condition would really correspond to the empirical result on basal metabolism shown in table 1 (p. 317) more than to the surface law.

The influence of body size on metabolism may reasonably be related to oxygen transport, but no evidence can be found from these theoretical considerations that the metabolism of animals is more closely related to their geometric surface than to some other function, as for example the $\frac{3}{4}$ power of the body weight.

Biological Explanation of the Relation Between Body Size and Metabolism.—From the interspecific point of view, two of the four kinds of explanations for the influence of body size on metabolism stand criticism: regulation of a constant body temperature, and geometric and dynamic relations of oxygen transport. But neither the outside temperature alone nor the intensity of blood flow determines the metabolism. Lehmann (1926, p. 577) writes that the metabolism of an organ is not increased if it gets more oxygen, but that more blood is brought to the organ if it requires more oxygen. This teleological statement, however, is not an explanation either.

The biological theory is that those animals are the fittest in natural selection in which the metabolism is so regulated that the requirements for maintaining a constant body temperature and the energy requirements for the necessary mechanical work are in an economical relation with the geometric and dynamic possibilities of oxygen transport.

In the introduction, I claimed as a working hypothesis that there was a general influence of body size on metabolism, leaving the question open as to how this influence might be formulated. Neither the empirical results from table 1 (p. 317) nor the discussion of the theory of the surface law gave evidence for the belief that the rate of metabolism is more closely related to the body surface than to some other function of the body size. The general formulation of the law of body size and metabolism is that the logarithm of the metabolism is proportional to the logarithm of body weight.

Deduction.—The reason for the excursion into the theory of the surface law was the discrepancy between the surface law and the empirical results in table 1, based on the recent work on metabolism. The study of this theory fails to show that there is any evidence for a

closer relation of metabolism to the geometrical surface of animals than to some function of the body weight; for example, the $\frac{3}{4}$ power, which is in better agreement with the empirical results in table 1 (including ruminants).

APPLICATION OF RESULTS

The Unit of Body Size for Measuring the Relative Rate of Metabolism.— It follows from the result of metabolism studies as well as from the discussion of the theory of the surface law that metabolism can be related to a power function of the weight, and the unit of body surface given up. There are two reasons for hesitating to do so. First, the best-fitting power function cannot yet be given definitely. Further investigation may show that some unit other than $W^{3/4}$ may be preferable. Secondly, the unit of body surface has been relatively long in use, and much work has been done to develop it. Even if the theoretical and empirical weakness of the surface law is admitted, it may be preferable to keep the square meter of body surface as a unit of measurement as long as it proves to be useful, and especially if it meets the first requirement of any unit for measurement, namely, to be well defined. It seems, however, that the more work done to determine the surface area, the less is one able to define the unit of it for the measurement of metabolism.

The simplest method of determining the surface area of an animal was probably that of Richet (1889, p. 221). He calculated the surface from the body weight assuming the animals to be spheres. If a specific gravity of 1.0 is considered, the calculation of Richet would be:

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

where S = surface in square centimeters
W = body weight in grams

Meeh attempted to get a closer approximation of the true surface of the animal by choosing different parameters of the $\frac{2}{3}$ power of the weight instead of the sphere-constant 4.84. Meeh writes:

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

where S = surface in square centimeters
W = weight in grams

and where k varies according to the different species of animals and seemingly even within one species; in man for example from 9 to 13, as Harris and Benedict (1919, p. 142) show in their history of the development of the unit of body surface. A table of the different Meeh factors is given by Lusk (1928, p. 123).

Later on, not only were different coefficients suggested, but also the exponents of the power function were varied. In addition ingenious methods have been developed to measure the surface area directly.

The natural question as to which of the different methods of determining the surface area gives the closest results for the true surface leads to a serious difficulty. What does belong to the true surface and what does not belong to it? In trying to answer this question one finds that not only the skin is elastic[11] but also the conception of its geometrical surface area on the living animal, and that fact, for this particular question, is worse. But suppose it would be possible to define exactly a true surface geometrically and to confirm what is indeed to be expected —namely, that the elaborate modern methods would allow us to determine the true surface area with a higher degree of accuracy than Richet's formula—the second question still remains: Is the morphological improvement in this case of physiological significance?

As early as 1884 D'Arsonval (cited by Harris and Benedict, 1919, p. 136) stated that the physiological surface of the animal was not the same as the "physical." The ventral part of the skin of an animal living outdoors which radiates to the ground may have a heat loss very different from the dorsal part radiating to the sky. A similar view has been expressed by Carman and Mitchell (1926, p. 380). In order to be exact, the different rate of radiation resulting from different colors of the covering should be considered. Begusch and Wagner (1926) indeed claim that the heat output of dark-colored guinea pigs is 124 per cent of that of light-colored guinea pigs; and recently Deyghton (1929, p. 151) put forward a similar idea, mentioning that, according to de Almeida, negroes in Brazil had a metabolism about 8 per cent higher than that of white men. These statements, especially in their relation to the color of the skin, may not be above criticism (see Du Bois, 1930, p. 222), but certainly Benedict and Talbot (1921, p. 160) are correct in writing that: "The physical and physiological factors influencing the heat loss from the surface of the human body are so different at different parts of the body as to preclude any generalization that equal areas result in equal heat loss."

It might be thought that on the average the "physiological surface" would be a constant part of the geometrical surface; and for an approximation this supposition is probably correct; but there does not seem to be enough reason for the belief that this proportionality is so accurate as to justify improvements in methods or formulas which allow the

[11] Mitchell (1929, p. 440) found the area of the skinned carcass of the rat to be 430 sq. cm. The unstretched skin measured 536 sq. cm. A moderate stretching increased the area to 630 sq. cm.

determination of a "true" geometric surface area with a few per cent less variation than has been possible hitherto.

If a cat is curled up for sleep, as it is during a considerable part of its life, the calculation of its surface as a sphere is, from the point of view of heat loss, probably better than the improved calculation according to Meeh, because in the latter case one calculates the ventral part of the skin as surface, although in the curled position this is certainly not a cooling surface comparable to the dorsal part.

Thus, even if the surface of the skin were well defined, the improvements in measuring it may not be significant for the question of body size and metabolism.

The development of as many different formulas for calculating the surface as there are species concerned, or even more, physiologically not only is a doubtful improvement but has a definite *disadvantage.* The present situation in reducing the metabolism to the unit of body surface is similar to the general condition of measuring lengths in the Middle Ages when the size of the foot varied from country to country and in referring to a certain length, one therefore had to be sure which foot was used. This situation is present in measuring the metabolism even within one species. If it is stated, for example, that a steer has a metabolism of m calories per square meter of body surface, it is necessary to find out whether that surface area has been calculated on the basis of Meeh's formula and, if so, which constant has been used. The calculation may have been made according to Moulton, or according to Hogan's formula; it is also possible that the author has a formula of his own, or that he determined the surface of his steers directly. And if the method of determining the surface is known, further difficulty arises when one attempts to compare this result with others also obtained on steers, but on the basis of different methods for the surface determination.

One may readily come to the conclusion that improvements in determination of surface lead to a labyrinth, and that it might be better to go back and relate the metabolism to the unit of body weight, giving up the comparison of the metabolism of animals so different in size that the reduction to the unit of weight might imply a considerable error. This has recently been done by Benedict and Riddle (1929) in their work on the metabolic rate of pigeons. But this step out of the chaos should be the start rather than the end. Benedict and Riddle also use a common unit, the weight; they can do so as long as their individuals are similar in size. But they cannot, for example, directly compare the metabolism of ring doves and pigeons. And if within one species they had material with large variations in body size, the question would also arise whether it is correct to calculate on the basis of the

proportionality of metabolism to weight. In a good deal of metabolism work this question cannot be avoided. The comparison of the metabolism of different animals cannot be given up, and therefore the search for a common basis for comparing the metabolism of animals different in size cannot be given up; for on this basis alone can studies be made of other influences on the metabolism, such as age, sex, and condition of body.

Krogh (1916, p. 140) has proposed to reduce the metabolism to the unit of W^n instead of the body surface. Stoeltzner (1928) uses the same unit when he calculates for medical purposes the energy requirement of man as $160 \times W^{2/3}$. Brody, Comfort, and Mathews (1928, p. 23) also prefer the use of a power function of the weight as a unit for calculating the metabolism. The last-mentioned authors write: "We do not quite see the logic involved first in relating area to body weight, then computing area from body weight, and finally relating heat production to the computed area. Why not relate heat production to the body weight directly?" Mitchell's objection (1930*a*, p. 444) to this proposal is that it ignores the physical significance of the relation between surface and heat production. Indeed, the empirical result that the metabolism is proportional to a power function of the weight is independent of any theory about the physical background of this relation.

But the use of W^n as the unit of body size for metabolism does not necessarily exclude a physical significance of the relation between surface and heat production. If the surface is calculated according to Richet as $4.84 \times W^{2/3}$ and if the heat loss is proportional to the surface, it is, as a matter of course, also proportional to $W^{2/3}$. A real difference in opinion can occur only if the surface of different animals cannot be expressed as the same power function of the weight.

The surface per unit of $W^{2/3}$, or the Meeh constant $\left(k = \frac{S}{W^{2/3}}\right)$ is a measure for a relatively large or small surface of animals; this term, which is about 10 for most animals, goes up as high as 13 for the rabbit, showing the influence of its large ears. Calculating the metabolism simply to the $\frac{2}{3}$ power of the body weight, an abnormally high value for the metabolism of rabbits would be expected. This is not the case. Voit (1901, p. 116) found a basal metabolism for the rabbit of only 776 Calories per square meter using the Meeh formula $S = 12.9\ W^{2/3}$. It is to be stated, however, that the value of 776 is still too high. Voit writes that this value would have been much lowered had he averaged all data available on the basal metabolism of rabbits. If the area of the ears is subtracted from the body surface, the metabolism of the

rabbit fits better into Rubner's scheme of 1,000 Calories per square meter, for it is then 917 Calories (Lusk, 1928, p. 124). In determining the surface of the rabbit, it is therefore doubtful whether or not the area of the ears belongs to that surface. This means a difference of 20 per cent, and it may be asked: What do we gain if we can develop a method which allows us to determine the surface area to within few per cent accuracy, if an amount of 20 per cent is in any way doubtful? A physiological reason may be found for subtracting the area of the rabbit ears from its total surface area, but what remains of the surface law if corrections of this kind have to be made? What remains is in accordance with the empirical result of table 1: A general influence of body size on the metabolism which may be related to W^n as well as, or even better than, to the actual surface.

It may therefore be concluded: Although no definite power function of the body weight can as yet be given as the best unit to which the metabolism of animals which differ in size may be calculated, there is reason to give up the unit of body surface because it is not well defined and because its strict application tends to obscure rather than to clear up the knowledge of the influence of body size on metabolism. Any unit of body weight from the $\frac{2}{3}$ up to the $\frac{3}{4}$ power is preferable to the unit of body surface because a power function of the body weight is so much better defined than the unit of body surface and because its general application to all homoiotherms opens such a wide field from the point of view of comparative physiology that even considerably greater deviations from the mean by the use of W^n instead of the surface, would be outweighed.

The Intraspecific Application of the Interspecific Results.—The best-fitting unit of body size for comparing the metabolism of rat, man, and steer has been found to be $W^{3/4}$. Is there objection to using this unit for comparisons within one species?

From a table on the metabolism of dogs given by Rubner (1928, p. 164) it follows that the metabolism per square meter of body surface is on the average somewhat higher in the smaller dogs than in the larger ones. The coefficient of tendency, the term τ (see p. 320), is in this case -0.362 per cent of the mean.

From another table by Kunde and Steinhaus (1926, p. 128) giving also results obtained on dogs by Rubner the contrary conclusion would be drawn, namely a larger metabolism per square meter of body surface in the larger dogs, the term τ being $+0.200$. As Rubner calculated the surface on the basis of Meeh's formula, the result is applicable also for the $\frac{2}{3}$ power of the weight.

Figures given by Richet (1889, p. 222) for the metabolism of rabbits show that the metabolism per unit of $W^{2/3}$ is decreased with increasing body weight. These data, as well as the first-mentioned table of Rubner, though confirming the general influence of body size on metabolism and the theory that this influence is more closely related to the $\frac{2}{3}$ power of body weight than to body weight directly, seem to be in contradiction to the more special interspecific result, that the best-fitting unit of body weight is from $W^{0.72}$ to $W^{0.74}$ or approximately the $\frac{3}{4}$ power.

As age and body condition (especially fat content) were not taken into consideration, their data do not indicate whether or not the heavier animals were on the average also the fatter and older ones. Hence no conclusive answer to the question with regard to rabbits or dogs can be obtained though these two species would be especially suitable for intraspecific studies on the relation of body size and metabolism.

The data on the 136 men in the biometric study of Harris and Benedict (1919, p. 40, ff.) have been arranged in eight groups according to body weight. The age was well equalized among these groups. The same has been carried out for the 103 women. In this case the group of the heaviest women has been omitted from calculation because the average age of this group was much higher than the average age of the other groups. The average metabolism and weight of those groups have been submitted to the same calculation as the data on the thirteen groups in table 1. The result of this calculation is shown in table 7.

TABLE 7

BASAL METABOLISM OF HUMAN BEINGS
CALCULATED TO DIFFERENT UNITS OF BODY SIZE

Unit of body size	Average basal metabolism Cals. per 24 hours per unit of body size		Coefficient of tendency in per cent of mean (τ)	
	Men	Women	Men	Women
W (Body weight)	25.7	25.3	−0.537	−0.778
$W^{3/4}$	72.5	67.8	−0.188	−0.339
$W^{0.7}$	89.1	82.7	−0.108	−0.242
$W^{0.6}$	134.9	122.9	+0.053	−0.056
$W^{0.5}$	205.5	182.7	+0.302	+0.130
$S = 12.31 \times W^{2/3}$ (Meeh)	830	767	−0.040	−0.177
$S = W^{0.425} L^{0.725}$ (DuBois)	925	857	+0.158	+0.125

The two main results obtained by interspecific comparison seem to be confirmed within the human species: (1) the metabolism is more closely related to the surface or to the $\frac{2}{3}$ power of the weight than to its first power; (2) there is no evidence that the surface of the skin is a better unit for the calculation of the metabolism than some power function of the weight would be.

The best-fitting unit for calculating the metabolism of human beings seems to be a power function close to $W^{0.6}$. This is not in accordance with the result obtained by interspecific comparison where the term $W^{0.72}$, or even $W^{0.74}$, if ruminants are included, was found to be the best fitted.

As already mentioned, the results in table 7 within the human species may be obscured by the influence of other factors. I have attempted to eliminate two of those factors by calculation, namely *age* and *build*, the two influences which are considered besides weight in the regression equation of Harris and Benedict for the prediction of human metabolism.

The calculation has been carried out as follows:

Influence of Age in Man.—The influence of age on the metabolism has been calculated from the material which Benedict (1915, p. 284) has selected for this purpose. Three results have been omitted in order to get rid of the possible influence of stature. The calculation is shown in table 8.

TABLE 8

AGE AND METABOLISM IN MAN

Group	Age		Weight, kg.	Height, cm.	Specific stature*	Total Cals. per 24 hours
	Range	Average years				
Average of 14 men	16–41	26.0	60.3			1,578
7 younger men	16–24	20.3	60.9	168	42.9	1,631
7 older men	26–41	31.7	59.7	168	43.1	1,525
Difference		11.4	−1.2	0	0.2	106
Difference due to weight†						23
Difference due to age						83

Difference due to age per year $= \frac{83}{11.4} = 7.3$ Cals.

Per cent of average metabolism (coefficient of age) $\frac{7.3}{1,578} \times 100 = 0.46$ per cent.

* For definition see p. 343.

† The correction for the difference in weight has been calculated on the basis of the equation $\frac{dM}{dW} = 0.73\frac{M}{W}$ (see p. 320) which was derived from table 1.

From a graph given by Harris and Benedict (1919, p. 120) it may be concluded that the heat production per square meter of body surface decreases in men 0.37 per cent of the average (926 Cals.) for each year increase in age; the corresponding figure for women is 0.34 per cent.

The advantage of obtaining the coefficient of age on 14 men as described above is that other influences are well excluded. The advantage of the last-mentioned figures is that they are obtained from a larger number of individuals.

Considering the variations which are to be expected, the second place of the figure may be omitted, the decrease of metabolism per yearly increase in age assumed to be 0.4 per cent of the metabolism at the age of 30.

The metabolism differs according to whether a person is stout or slim, as suggested by Benedict. Stature is no adequate measure for an influence of that kind, for it depends on weight itself; stature must be considered in relation to body weight.

In animals of different size which are similarly built, the quotient of body length (or height in man) and body weight would still depend on weight. The smaller the animals the larger it would be. A good unit, however, which expresses in one figure how stout or slim an individual is, and which is independent of the body size, is the quotient of body length (L) in centimeters divided by the cube root of body weight (W) in kilograms. This term $\frac{L}{W^{1/3}}$ may be called the *specific stature.*[12] As the weight is proportional to the volume, the cube root of it is proportional to a linear dimension, thus the specific stature is a term without dimensions.

In order to determine the influence of build on the metabolism, the results on the 136 men reported by Harris and Benedict (1919) have been arranged according to the specific stature into two groups, as shown in table 9.

TABLE 9

INFLUENCE OF SPECIFIC STATURE ON METABOLISM IN MAN

Group	Specific stature $\frac{L}{W^{1/3}}$	Body weight, (W), kg.	Height (L), cm.	Age, years	Calories produced in 24 hours			
					Total	per $W^{2/3}$	per $W^{0.7}$	per $W^{0.75}$
Average, 136 men	43.4	64.1	173	27.0	1,631	102.0	88.8	72.2
68 slim men	44.8	59.1	175	25.9	1,567	103.3	90.1	73.5
68 stout men	41.9	69.1	172	28.1	1,695	100.7	87.6	70.9
Difference	+2.9	−10.0	+3	−2.2	−128	+2.6	+2.5	+2.6
Difference due to age*					− 14	−0.9	−0.8	−0.6
Difference due to specific stature					−142	+1.7	+1.7	+2.0
Difference per unit of specific stature						+0.59	+0.59	+0.69
Per cent of the average (coefficient of build)						*per cent* +0.58	*per cent* +0.66	*per cent* +0.96

* 2.2x0.4 per cent = 0.88 per cent of the average.

[12] The inverse of the specific stature has been used by Pirquet and adopted by Cowgill and Drabkin (1927, p. 41) as a measure for the state of nutrition.

The coefficient of build, i.e., the per cent variation in metabolism per unit of variation of specific stature, differs according to whether the influence of size is assumed to be related to the $\frac{2}{3}$ or to the $\frac{3}{4}$ power of the weight, because, on the average, the heavier persons are also the stouter and probably fatter ones.

If the average metabolism of the 8 groups of men mentioned on page 341 is reduced to the same age and the same build by means of the coefficient of age of 0.4 per cent and a coefficient of specific stature of 1 per cent, then the logarithmic relation between body weight and metabolism may be calculated as shown in table 10.

TABLE 10

LOGARITHMIC RELATION BETWEEN BODY WEIGHT AND METABOLISM IN MAN

Group	W	Average log W	Cals. corrected	Log of corrected Cals.
Average 136 men	64.1		1,635	
68 light men	56.3	1.74816	1,495	3.17422
68 heavy men	71.9	1.85460	1,775	3.24802
Difference		+0.10544		+0.07380

$$\frac{\Delta \text{ (log calories)}}{\Delta \text{ (log } W)} = \frac{0.0738}{0.10544} = 0.70$$

From this calculation the best-fitting unit of body size for comparisons of metabolism within the human species appears to be $W^{0.70}$. The analogous calculation by the use of the coefficient of specific stature of 0.58 per cent shows $W^{2/3}$ as the best-fitting unit.

From the result just mentioned the $\frac{2}{3}$ power of the weight seems preferable to the $\frac{3}{4}$ as unit for human metabolism. A conclusive answer on the question which of the two power functions fits better cannot, however, be given on the basis of the available data. Both the $\frac{2}{3}$ power of weight with a coefficient of build of 0.6 per cent and the $\frac{3}{4}$ power of weight with a coefficient of build of 1 per cent may be tested by their accuracy in predicting human metabolism.

For that purpose the metabolism is formulated in the following equation:

$$M = c \times W^n(1+a(A-a)+\varphi(s-S)+\ldots\ldots)$$

where

M = basal metabolism at temperatures above the critical
c = coefficient of species and sex
W = body weight
n = exponent $\frac{2}{3}$ or $\frac{3}{4}$
a = coefficient of age
A = standard age (arbitrarily chosen constant)
a = actual age
φ = coefficient of build
S = standard specific stature (arbitrarily chosen constant)
s = actual specific stature

This equation expresses three assumptions:

(1) That the metabolism of a person of standard age and specific stature has a metabolism proportional to the nth power of its body weight.

(2) That for each year above or below the standard age, the metabolism is decreased or increased by the same part a of the metabolism at standard age and build.

(3) That for each unit of specific stature above or below the standard specific stature, the metabolism increases or decreases by the same part φ of the metabolism at standard age and build.

It may be found in later investigations that other influences can be measured and added to the equation—for example, the relative fat content of the body, which is now considered only insofar as it influences the specific stature.

The factor c has been obtained as follows:

The average weight of the 136 men in the study of Harris and Benedict (1919, p. 57) was 64.1 kg; the $\frac{3}{4}$ power of this average is 22.65. The total heat production per day was on the average (Harris and Benedict, 1919, p. 67) 1,631.7 Cals.; thus the average heat production per unit of the $\frac{3}{4}$ power of the average weight was 72.04 Cals. This is for an average age of 27 years. For a standard age of 30 years the metabolism would be lower—namely, according to the coefficient of age previously developed, $\frac{72.04}{1+0.004\times 3} = 71.2$. This is the factor c for the calculation on the basis of $W^{3/4}$. The corresponding factor for $W^{2/3}$, calculated similarly, is 100.7. The standard build has been calculated by dividing the average height by the $\frac{1}{3}$ power of the weight. The prediction equation for the metabolism of man is thus obtained:

(1) $M = 71.2\times W^{3/4}[1+0.004(30-a)+0.01\ (s-43.4)]$
(2) $M = 100.7\times W^{2/3}[1+0.004(30-a)+0.006\ (s-43.4)]$

The analogous calculation has been applied to the data on the 103 women in the study of Harris and Benedict. The prediction in this case may be made according to the equations:

$$M = 65.8 \times W^{3/4}[1+0.004(30-a)+0.018\ (s-42.1)]$$
$$M = 92.1 \times W^{2/3}[1+0.004(30-a)+0.014\ (s-42.1)]$$

The daily heat production predicted according to the four equations was compared with the corresponding data actually observed. In order to show the influence of correction for age and specific stature on the accuracy of prediction, the uncorrected heat production on the basis of the power function of the weight was also compared with the actual heat production.

The average deviation between predicted and observed heat production, irrespective of the sign in per cent of the observed heat production, is given in table 11 together with the square root of the mean square deviation of the observed from the predicted. The corresponding data resulting from the prediction of the metabolism by the regression equations of Harris and Benedict are added for comparison.

TABLE 11

ACCURACY OF PREDICTION OF HUMAN METABOLISM

Basis of calculation	Sex	Formula	Average deviation $\frac{\Sigma d}{n}$	$\sqrt{\frac{\Sigma d^2}{n}}$
$W^{3/4}$ corrected for age and build	Men	$M = 71.2 \times W^{3/4}\ [1+0.004(30-a)+0.01(s-43.4)]$	4.90	6.16
$W^{2/3}$ corrected for age and build	Men	$M = 100.7 \times W^{2/3}\ [1+0.004(30-a)+0.006(s-43.4)]$	5.00	6.17
Harris and Benedict 1919	Men	$M = 66.4730+13.7516\ W+5.0033L-6.7750a$	4.98	6.23
$W^{3/4}$ uncorrected	Men	$M = 71.2 \times W^{3/4}$	6.16	7.72
$W^{2/3}$ uncorrected	Men	$M = 100.7 \times W^{2/3}$	6.01	7.55
$W^{3/4}$ corrected for age and build	Women	$M = 65.8 \times W^{3/4}\ [1+0.004(30-a)+0.018(s-42.1)]$	6.42	7.94
$W^{2/3}$ corrected for age and build	Women	$M = 92.1 \times W^{2/3}\ [1+0.004(30-a)+0.014(s-42.1)]$	6.37	7.84
Harris and Benedict 1919	Women	$M = 655.0955+9.5634\ W+1.8496L-4.6756a$	6.27	7.88
$W^{3/4}$ uncorrected	Women	$M = 65.8 \times W^{3/4}$	9.31	11.80
$W^{2/3}$ uncorrected	Women	$M = 92.1 \times W^{2/3}$	8.53	11.42

There could hardly be a better recommendation for either one of the four equations developed herein than the fact that they predict the metabolism with practically the same degree of accuracy as the empirical regression equations of Harris and Benedict (1919, p. 227).

The criticism of Krogh, presented by Boothby and Sandiford (1924, p. 80) that the terms of Harris and Benedict are of purely statistical nature does not apply to the equations developed in this paper; the coefficients in the latter equations have a certain physiological meaning.

Reducing the equation for the women to the average specific stature of men, the two results can be compared directly:

$$\text{for women } M = 67.4 \times W^{3/4}[1+0.004(30-a)+0.018\ (s-43.4)]$$
$$\text{for men } M = 71.2 \times W^{3/4}[1+0.004(30-a)+0.010\ (s-43.4)]$$

where

W = weight in kg
a = age in years
s = specific stature = $\dfrac{\text{stature in cm}}{\text{weight}^{1/3}}$

On the basis of the same specific stature the ratio of the metabolism of men and women would therefore be as 71.2:67.4=1:0.95. Without reduction to the same specific stature the ratio is wider—namely, 71.2:65.8=1:0.93, because on the average the women have a lower specific stature.

If the metabolism of the 136 men and 103 women studied in the Carnegie Nutrition Laboratory is reduced to a standard age and standard specific stature, any power of the body weight from the $\frac{2}{3}$ to the $\frac{3}{4}$ serves as well as or better than the unit of body surface for expressing the influence of body size on metabolism.

Therefore there is reason to apply for intraspecific calculation the same power of the weight (within the mentioned limits) which may by interspecific comparison be found the best.

GENERAL CONCLUSIONS

The result of recent work on the basal metabolism of different species and the critical review of the fundamentals of the surface law leads to the suggestion that the surface law should be replaced by a weight-power law. A power function of the body weight gives a better-defined unit for measurement than the unit of body surface.

From comparison within the human species it follows that the metabolism may be formulated thus:

$$M = C \times W^n[1+\alpha(A-a)+\varphi(s-S)+ \ldots\ldots\ldots]$$

Not only is it probable that the metabolism of all homoiotherms may be expressed in the same scheme but it seems that the same exponent of the bodyweight (n) may be used for interspecific comparisons as well as for comparisons within one species.

Research on metabolism would be much more economical, i.e., less time-consuming, if the term W^n could be settled so that all authors would express their results on the same basis. This task would require further systematic experimental work, especially with regard to the critical temperature. It would call for international cooperation and agreement.

SUMMARY

A table with the results of recent work on metabolism of different animals from the ring dove and the rat to the steer shows a closer relation of the basal metabolism to the ¾ power of body wieght than to the geometric surface of the animal.

In order to study the question whether or not there is a theoretical reason for maintaining the surface of the skin as the basis for comparing the metabolism of animals which differ in size, four theories of the surface law, namely, temperature regulation, nutritive surface, compcsition of the bcdy, and rate of blood circulation, are discussed.

It is demonstrated that the animal can vary its specific insulation to a considerable degree, and that therefore an accurate relation between surface and heat flow, according to Fourier's Law, is not to be expected.

However, as the possibilities of altering the specific insulation are practically limited, the heat-loss theory for cold climates and the overheating theory for hot climates stand criticism for *approximate* comparison of the heat-production of animals which differ sufficiently in size.

Basing the surface law on the nutritive surfaces, the cell surfaces, or the protoplasm structures has been shown to be without warrant.

Differences in the composition of the body, inert fat, active protoplasm, and amount of blood, though unquestionably affecting metabolism, cannot explain the considerable influence of body size on the metabolism of different kinds of animals. The fact that the basal metabolism of warm-blooded animals is approximately proportional to the ⅔ or the ¾ power of the body weight is a matter governed by the organism as a whole; it cannot be derived from a summation of the vital functions of the cells or other parts of the body.

On the basis of the similarity in the building plan of all warm-blooded animals and of the limited velocity of muscular contraction, it may be conceived that the intensity of blood flow, and hence the intensity of oxygen transport to the tissues, is related more closely to a lower power of body weight than unity.

The biological explanation of the relation of body size and metabolism may be expressed as follows: In natural selection those animals are the fittest in which the caloric requirements are in harmony with the

hemodynamic possibilities of oxygen transport. This harmony seems to be established when the logarithm of the metabolism is proportional to the logarithm of body weight.

No theoretical evidence has been found to indicate that the metabolism of animals should be related exactly to the surface area of their skin.

For the sake of precision, the metabolism of animals should not be given in terms of body surface, because this term is not well defined.

A simple equation probably applicable to all homoiotherms and characterizing the metabolism by three coefficients (sex and species, age, specific stature) gives a prediction of the metabolism of man on the basis of the $\frac{2}{3}$ or the $\frac{3}{4}$ power of body weight with practically the same degree of accuracy as by the empirical regression equation of Harris and Benedict. This result strengthens the hypothesis that the intraspecific relation of body size and metabolism follows the same logarithmic rule as has been found by interspecific comparison.

It is suggested that the heat production of all warm-blooded animals should be expressed in terms of the same power of the body weight and that for the sake of economy in research the question of the best-fitting exponent ($\frac{2}{3}$ to $\frac{3}{4}$) should be studied in order to find a unit for measurement which might be adopted internationally.

ACKNOWLEDGMENTS

For assistance in preparing the manuscript, I am indebted to Dr. G. H. Hart, Dr. T. I. Storer, and Miss Helene Kirby.

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Submitted for publication July 2, 1931.